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A SPECULATIVE CONSIDERATION OF CERTAIN POSSIBLE FORMS OF SEXUAL SELECTION IN MAN

G. E. HUTCHINSON

Osborn Zoological Laboratory, Yale University, New Haven, Connecticut

The present contribution,¹ necessarily based on very incomplete information, is presented mainly because the subject appears to be important and because the implications of such data as exist seem to be little realized even by investigators in the fields to be discussed. It is hoped that its publication may stimulate research.

SELECTION

The total population of one generation of any organism is not derived equally from each member of the preceding generation. A certain number of individuals in any generation will be less fertile, others more fertile, than the mean. If any genotypes are more frequent among the less fertile portion of the population than in the more fertile portion, it is evident that one of three things must be happening. (1) There may be selection against the genotypes in question so that they become rarer, or (2) they may be maintained in the population by mutation in the face of selection, or (3) selection in favor of heterozygotes, or some other form of balanced polymorphism, may occur in the population.

PARAPHILIA

The human populations of Europe and North America, and probably of other parts of the world, contain a small group of people overtly exhibiting what is best termed *paraphilia*, namely a tendency to substitute in their sexual behavior, goals which cannot lead to reproduction, in the place of a

¹A preliminary statement of the fundamental idea was made in a somewhat generalized form in an earlier review of contemporary work on human evolution (Hutchinson, 1957). At the time of writing this earlier paper, I did not know of Kallmann's (1952 a, b) remarkable work on homosexuality in twins, which has led me to reconsider the entire problem. I am indebted to Dr. David Lack, Dr. D. F. Poulson and to Dr. E. S. Deevey, who read earlier drafts of the paper, to my wife for much helpful criticism, and particularly to Dr. Lawrence S. Kubie, who has subjected all my ideas to a most generous and intense critical evaluation. Almost no one agrees with the entire paper, but no critic believes it without value. The initial exploration of the problem was made during tenure of a John Simon Guggenheim Memorial Fellowship.

partner of the opposite sex. The two most important forms of paraphilia are homosexuality and fetichism. According to Kinsey, Pomeroy and Martin (1948) approximately ten per cent of the males of reproductive age in the United States exhibited only (group 6) or mainly (group 5) homosexual behavior for at least three years, at a time prior to interview. Among women, the incidence is supposed to be much lower, amounting to a proportion of the order of one per cent. (Kinsey, Pomeroy, Martin and Gebhard, 1953). With regard to fetichism, the same authors merely say that individuals "who respond only or primarily to objects which are remote from the sexual partner, or remote from overt sexual activities with a partner, are not rare in the population." The phenomenon in its patent form is usually regarded as almost exclusively masculine. It is evident that, although the data are imperfect, if any genetic basis for these conditions exists, they are common enough to play a considerable part in the demogenetics of the population as a whole.

FERTILITY

At present, any conclusion as to lowered fertility in paraphilia is largely a presumption, though a reasonable one. The data of Kinsey and his co-workers obviously cannot allow for possible changes in behavior after their interviews, so that to assume that all the group 6 homosexuals (exhibiting only homosexual behavior) are non-fecund is erroneous. Kallmann (1952 a, b) found that, in a population of 85 twin homosexual men of median age over 26, all rated as belonging to group 3 or higher (that is, at least as homosexual as heterosexual, or more so) only 11 had contracted marriages. These marriages were mostly short-lasting. Three of the marriages had produced children. In no case of the five children born is the biological paternity certain beyond reasonable doubt. This fertility looks very low, but cannot be properly evaluated without more data on age structure. Davis (1929) observed a supposedly significantly greater proportion (38.8 per cent) of childless marriages among married women who admitted to post-marital homosexual activity than in her overall sample (20.8 per cent). The average age at the time of reply was 38.2 years in the case of the small (18) homosexual sample, 38.3 years in the case of the large (1000) overall sample. Such meager evidence supports the commonsense view that homosexuality in western cultures is likely to be correlated with a low fertility.

With regard to fetichism, there is no information of particular value. The extreme cases reported in the clinical literature are often obviously psychologically sterile, but there are also doubtless plenty of men with markedly fetichistic tendencies who achieve normal-sized families. One may presumably assume continuity between the two groups, which of itself implies a somewhat lower fecundity, though it is not possible even to guess how great the effect might be.¹

¹Kubie (*in litt.*) suggests that in the cases of "bisexual" homosexuals or fetichists who marry, there may be an unconscious tendency to avoid coitus during the more fecund parts of the menstrual cycle, so reducing fertility.

Though it seems evident that various forms of paraphilia are common enough to be significant in demogenetics and that part of this significance is likely to depend on lowered fertility, any importance that the condition may have in the genetics and evolution of human populations, will be dependent not only on frequency and low fertility, but on some degree of genetic control. At the present time, this is the aspect of the problem that is hardest to treat.

GENETIC DIFFERENCES IN TEMPERAMENT

Some introductory remarks on the general problem of the inheritance of temperamental differences are necessary before proceeding to a discussion of the one body of work that is relevant to the details of the present discussion. The pioneer students of sexual as well as other kinds of psychopathology in the late 19th century, usually assumed an hereditary predisposition to account for any condition whose genesis they did not understand. The high selection rate that would obviously be operating against some of the supposedly inherited conditions that they considered, seems not to have worried a generation that knew nothing of the magnitude of mutation rates nor of the mathematical theory of selection in natural populations.

During the present century, the ascendancy of psychoanalysis in clinical psychiatry and of various types of behaviorism and learning theory in academic psychology, has led to a tendency to dismiss all genetic causes of variation in human behavior. This has probably happened for several reasons. Firstly and most respectably, it might be claimed that since fairly satisfactory explanations of a great variety of different types of behavior have been given in terms of upbringing and experience, no hypothesis of genetic control should be introduced unless it can be shown to be necessary. So far as psychoanalytic procedure goes, it is probably safe to say that the ordinary techniques employed are *per se* not logically capable of disclosing any facts that necessitate a genetic explanation; individual analysts, for reasons outside these techniques, may have suspected constitutional factors¹ to be operating in particular cases, though these factors are not necessarily genetic. The academic psychologist is well aware of what are commonly called species differences, as for example between the pigeon and the white rat, to name only examples from different classes. A sufficiently large array of similarities in diverse organisms has perhaps led to a tendency to underrate specific and individual differences, which in any case are not wanted in statistical experiments. Less respectably, environmental determination has seemed more amenable to manipulation and, therefore, more optimistic (from the standpoint of the manipulator). In the last two or three decades, it is probable that feelings of guilt have become associated with hatred of particular scapegoat groups; since most psychologists are decent and humane men, the hatred has been repressed and as a reaction all theories of genetic labelling of distinguishable groups of men have been suspect.

¹By constitutional in such cases is meant genetic factors together with such environmental factors as have operated prenatally.

When we examine the evidence that exists, the results are very difficult to evaluate. The most critical procedure consists in the statistical comparison of identical (uniovular or monozygotic) twins reared from infancy in different environments, as compared ideally with fraternal (binovular or dizygotic) twins also separated at infancy. The pioneer study of Newman, Freeman and Holzinger (1937) suggested, from a study of separated uniovular twins, that morphological characters were least likely to be altered by ordinary environmental influences, that formal intellectual characters as measured by intelligence tests were somewhat more modifiable, and that certain aspects of personality were quite easily modified. Neither their data, nor those of other studies, exclude genetic control of variation of personality, though they do seem to indicate that such control is of much less importance than in physical or formal intellectual characteristics. Criticism of this work in terms of the results of studies of twins reared together, as has sometimes been done, is quite improper and misleading. The intellectual justification of an extreme position in favor of almost complete environmental control of personality may therefore appear correct if we examine only human psychological data. Viewed against a wider background, it seems much less satisfactory.

Throughout the animal kingdom there are examples of genetic control of every kind of function including behavior, while in man there are good examples of genetic variability affecting every sort of character for which clear-cut evidence can be obtained. We are, therefore, practically obliged to assume that, if traits of personality in the widest sense are not in part genetically determined, there is some mechanism operating to screen the learning human being from the effects of genetic diversity. The existence of such a screen would be all the more remarkable in view of the inadequate screening provided against learning the wrong thing or the right thing at the wrong time. Data such as those of Newman, Freeman and Holtzinger do suggest that such a screen is in fact partly developed; even in an imperfect form, its existence is obviously a very important datum for the student of human evolution. At least the present writer would find the assumption of an *almost perfectly-developed homeostatic mechanism*¹ of this kind a more difficult assumption than to believe that there is some genetic determination of variation in affective behavior, even if psychotherapeutic techniques cannot by their very nature tell us of the existence of variation in the genetic background. Some degree of behavioral independence from genetic control may perhaps be implied by the general adaptability of mammals as compared with other vertebrates.

HOMOSEXUALITY IN TWINS

We may now turn as unprejudicially as possible to the main study of modern times suggesting a strong genetic determination of paraphilia. Kallmann

¹It is to be noted that the existence of homeostatic mechanisms always gives the initial impression of false simplicity.

(1952 a, b) has obtained data for the twin brothers of 40 uniovular and 45 binovular homosexuals all rated as in groups 3-6. In the binovular group, there were 26 male twin sibs, of whom 15 were entirely heterosexual, ten exhibited moderate homosexuality (group 1-4) and only one was almost exclusively homosexual (group 5). These proportions are not significantly higher than in the population at large. Of the uniovular sibs, three were deceased or unavailable, all the other 37 were homosexuals of groups 3-6. Nineteen uniovular homosexuals of group 6 had twin brothers rated as in groups 5 and 6; the twin of the twentieth member of this group was unavailable. Of the ten uniovular members of groups 3 and 4, nine twin brothers were available and were rated as belonging to groups 3 to 5, none being quite exclusively homosexual. Both active and passive twin pairs were noted in the uniovular cases.

Since these data refer for the most part to individuals reared together in infancy and to a varying unspecified age, they do not have the critical significance of studies on twins reared wholly apart after adoption.

The main difficulty in accepting the work lies in the possibility that being raised as a twin might in itself predispose an individual to homosexuality. Dr. Kubie (*in litt.*) points out that a prohibition not to play with one's own genitalia might be interpreted by a twin child as permission to play with the genitalia of the other twin. Mutual homosexual seduction might, therefore, be particularly likely in unisexual pairs of twins. Such a process would ordinarily have been forgotten at the time of interview in adult life and is not, therefore, inconsistent with Kallmann's emphatic statement that none of his twin pairs had ever engaged in homosexual practices *inter se*. It is possible that the somatic identity of the two members of a uniovular pair might facilitate such a process, but it is by no means obvious that it would produce the very great difference between the identical and fraternal pairs recorded by Kallmann. The latter does not give any details of the criteria used in determining whether his twins were mono- or dizygotic, nor does he say whether the criteria were applied before or after the rating for homosexuality had been made. There may have been some opportunity for the operation of unconscious subjective factors. The writer is inclined to accept the findings provisionally as indicating at least some genetic determination, though probably not as much as would appear at first sight. An investigation of the incidence of homosexuality among single uniovular and binovular twins would probably indicate if twinning *per se*, and in particular uniovular twinning, promoted the condition. This would doubtless be easier than the extremely difficult procedure of Kallmann. Such an investigation would throw no light on the problem independent of Kallmann's data, but would tend to validate the latter if no differences were found. The still easier study of marriage rates, if the samples were large enough to compensate for inevitable loss of information, might provide some significant results. As far as the writer can determine, even this has not been done.

For fetishism, we have no comparable data. Greenacre (1955) says she is not impressed by the possibility of any constitutional disposition towards

the condition, but the analogous point of view would have been taken by many psychoanalysts discussing homosexuality prior to or even in view of Kallmann's work.

GENETICAL INTERPRETATION

The only way of reconciling Kallmann's findings with the inevitable high rate of selection against the genotypes apparently partly responsible for paraphilia is to suppose that the modal type in the population is genetically unstable and that the individuals of presumed low fertility predisposed to paraphilia represent largely homozygous recombinations which are constantly being eliminated without changing the average genetic constitution of the population. To suppose that a process of progressive elimination of paraphilia is occurring would hardly be in accord with historic evidence, and would raise the difficulty of providing an explanation as to how the genotypes involved reached their former high frequency. The proportion of the population concerned seems to make a hypothesis of mutation exceedingly improbable.

The obvious model implies a situation not unlike that which Penrose (1955, cf. Goodhart, 1957a, Hutchinson, 1957) believes to underlie the population genetics of intelligence. The model is a special case of that developed by Goodhart (1955, 1957b) considering all possible types of genetic infertility. It bears formal similarities to the much more extreme type of determination of the fertile caste in the bee *Melipona* in which queens in most species must be heterozygous for three genes (Kerr, 1950a, b).

THE ORIGINS OF HOMOSEXUALITY AND FETICHISM

The classical psychoanalytic theory of the development of homosexuality in males involves an attempt on the part of the growing child to solve the conflict of the Oedipus situation by identifying with the mother and so in effect replacing the rivalry of the father by love directed by the father to the mother. One gets an impression from the literature that this is most likely to happen when there is strong maternal dependence in the pregenital and early genital stages of development.

The classical psychoanalytic theory of fetichism is that it represents an attempt to deal with the male child's fear of castration, which he develops when he becomes aware of the anatomical difference between the sexes. The fetichist is thus a man who unconsciously tends to reject his early anatomical discovery, denying that women really lack a conspicuous external intromittent organ. The fetich is in fact a substitute for the missing female phallus.

Recent studies, admirably reviewed by Greenacre (1953) to whom much of our modern knowledge of the subject is due, suggest that extreme fetichism not only involves rather severe traumatic experience in the early genital stage of development (two-four years) but that traumatic experience, usually fever, nutritional disturbances and the like between the ages of 0.5 and 1.5 years, have made it difficult for the developing infant to establish an ade-

quate image of its own body. There is concomitantly a great deal of clinging maternal dependence, and identification with the mother or other female member of the household. The highly disturbed cases who come for analysis frequently exhibit homosexual and sadomasochistic tendencies. Greenacre concludes that the various forms of paraphilia are closely interrelated in origin. Both homosexuality and fetishism involve a partial or complete rejection of a realistic view of women; in both cases there seems to be an early excessive dependence on and identification with a woman. Such a conclusion is probably valid even if some of the details as to how the conditions arise are still controversial.

It is important to realize that latent homosexual and fetichistic tendencies always seem to be present in human beings. Any genetic mechanism must be involved only in determining whether they are of such a kind as to lead later to particular kinds of action.

PSYCHOANALYTICAL INTERPRETATION

The best way of reconciling Kallmann's findings with those of the psychoanalysts (whose theoretical formulation Kallmann himself, for reasons that seem to me inadequate, appears to distrust) is to suppose that the genotypes responsible for a tendency to paraphilia operate primarily on the rates and extent of development of the neuro-psychological mechanisms underlying the identification processes and other aspects of object relationships in infancy. Such an hypothesis would be in accord with a great deal of modern embryological genetics, in which the genetic control of rates of various processes rather than the control of the mere existence or non-existence of the processes is usual. Along these lines, it is to be noted that the variations to be explained are likewise not the clear-cut presence or absence of a trait, but its greater or lesser expression in action, when it may always be present as a verbally reportable subjective fantasy. The hypothesis also has the great merit of leaving the psychoanalytic theory, and in favorable cases the possibility of psychotherapy, untouched, though it provides a frame within which the theoretical model operates.¹ The probability of a number of different genotypes being involved fits well with Kallmann's impression of the considerable diversity of his material. It may also be noted that this diversity need not necessarily be expressed in homosexual or other paraphilic behavior. Some of the genotypes may exhibit no phenotypic differences, and there is a vast range of variation in such behavior not necessarily involving lowered fertility, that might be in part determined by the same system.

¹The at one time very popular theories of endocrine disturbance and the more extreme view that homosexuals are cytologically and psychologically female but somatically male, now seem very dubious. The former has been considered and found wanting by Ford and Beach (1951); the latter, which rests on equivocal findings relating to the sex ratio, has to be supplemented by *ad hoc* hypotheses explaining why other inherently less improbable types of intersexuality are so rarely observed. These remarks, however, are not intended to imply that endocrine factors may not be involved in determination of the maturation rates postulated as significant.

The suggestion that a rather basic type of psychological development is involved, which is likely to have pleiotropic effects in non-sexual behavior, is in line with Kallmann's belief, if I understand his somewhat arcane expressions correctly, that the observed phenomena represent dislocations of a relatively lasting nature of the whole personality structure. In his particular cases, only 18 out of 85 were diagnosed as sufficiently adjusted both socially and emotionally, but it must be remembered that twinning and the social pressures against homosexuality may well produce lack of adjustment independently of the genotype.

From a more general point of view, the main importance of this type of selection, if it exists, is that it is operating on developmental processes which must be almost exclusively human and have only rather remote analogues among the lower animals; the developmental processes, moreover, are such that, as has just been indicated, they are likely to have effects on the personality outside the specifically reproductive and sexual fields.

The main objection that can be raised against the present hypothesis is that in some societies homosexuality is said to be unknown, while in others it is said to be a universal form of extra-reproductive male activity. Actually, what we are really concerned with is the incidence of genetically determined psychological failure of functional heterosexuality. The permitted or institutionalized homosexuality of some cultures may involve far less rejection of the female than is found in homosexuals in western Europe and North America. It may rather be compared to the apparently regular homosexuality exhibited in nature by some mammals, notably giraffes (Innis, 1958).

The problem, from a cross-cultural point of view, is really whether for example (Ford and Beach, 1951) there exist among the Siriono, who are said almost never to practice homosexuality, or among the Aranda, where nearly all men are said to engage in homosexual practices, a small group of men psychologically unable to achieve fertile heterosexual unions. In our own society, extreme homosexuality is apparently a frequent concomitant of this; in other societies, the same kind of selection might take place in a somewhat different way. I have failed to find any information as to whether in societies in which homosexuality is supposedly absent there are anerotic men comparable to the anerotic (group X of Kinsey *et al.*, 1953) women in ours, or whether in societies tolerant of homosexuality some men are never heterosexual.

It has been suggested that the various idiosyncratic preferences that influence men in falling in love represent the normal expression of a phenomenon of which the pathological form is extreme fetichism (Binet, 1887; Grant, 1949). This point of view evidently either rejects the psychoanalytic theories of fetichism, or takes no account of the great importance of the human face as the first visual stimulus to which a definite response is given by the developing infant (Spitz and Wolf, 1946). There is, however, a certain number of specific and usually visual stimuli supplied by artifacts which tend to have erotic significance, which can become the objects of extreme

fetichism in pathological cases, but which are so widely used in some societies that they evidently play a normal if minor role in human behavior. In contemporary society, high-heeled shoes provide an obvious example; in the fifteenth century, the tall conical headdress with a veil, known as the hennin, was almost certainly another.¹

The significance of this sort of ornament is presumably to neutralize almost universal homosexual tendencies and castration fears which might otherwise impede reproduction. As such, it appears erotic and feminine, in spite of its hidden masculine significance. The term *cryptandric* is suggested to designate such ornaments and the behavior involved in their use. Cryptandric behavior may involve conscious modification of somatic characters, as in the foot-binding formerly practiced on upper-class Chinese girls. It is possible that a number of ornaments and practices employed by primitive as well as literate peoples are to be regarded as cryptandric; this is particularly likely of ornaments worn through artificial holes in the body. Darwin (1871) quotes from Livingstone a conversation between the latter and Chinsurdi, chief of the Makalolo in South Central Africa. When Livingstone asked why women wore a ring (*pelelé*) in the pierced upper lip, Chinsurdi replied "For beauty, they are the only beautiful things women have; men have beards, women have none. What kind of a person would she be without the pelelé? She would not be a woman at all with a mouth like a man but no beard." There is also an evident connection with certain kinds of charms used as protection against the evil eye, which are often overtly sexual though either male or female (see Hutchinson, 1955). Psychoanalytically, the fear of castration is supposed to underlie the fear of the evil eye (Jones, 1923). It is interesting that Greenacre considers that an excessive dependence on charms and other lucky objects is a feminine counterpart of masculine erotic fetichism in contemporary society.

Anyone who has recently examined his copy of Darwin's *Descent of Man* will have been struck by the curious disparity between his account of structures believed by him to be produced by sexual selection in non-human animals and his account of supposedly like structures in man. The animal cases mainly refer to epigamic characters in the male, which are now understood to be either specific or sexual recognition marks or to be used in threat-displays, often of a territorial kind. The human cases are very diversified, largely female, frequently artificial and of no obvious functional significance.

It is reasonably certain that sexual selection in man, if it has been the sort of evolutionary force that Darwin believed, has largely involved the face.² It might also be reasonable to suppose that certain exaggerated fe-

¹It is said that 20,000 women burnt their hennins as the result of the preaching of the French Carmelite Thomas Conecte in the first third of the century. After he was executed for heresy involving denunciation of clerical celibacy, the hennin returned to fashion for several decades.

²This will, of course, involve a great store of infantile memories and identifications.

male structural modifications, such as steatopygia, function in a cryptandric manner. A somewhat intermediate case between artificial cryptandric modification and such a genetically determined structure is provided by the umbilical hernia, not uncommon among the Bantu peoples in parts of southern Central and northern South Africa, which I was told in 1926 was regarded as very attractive in a girl. The resulting rather phallic protrusion obviously bears some resemblance to the scarifications so commonly used in Africa. Doubtless such a structure is one that could often be avoided by appropriate care during parturition, if it were not considered desirable.

If a certain amount of female cryptandric display, either structural or artificial, is very widespread in man, as seems possible, it may serve to neutralize the psychoanalytic effects of developmental rates, optimal in other ways, but reproductively sub-optimal in the absence of the display in question. This may explain the apparent differences in the epigamic character of man and most other animals.

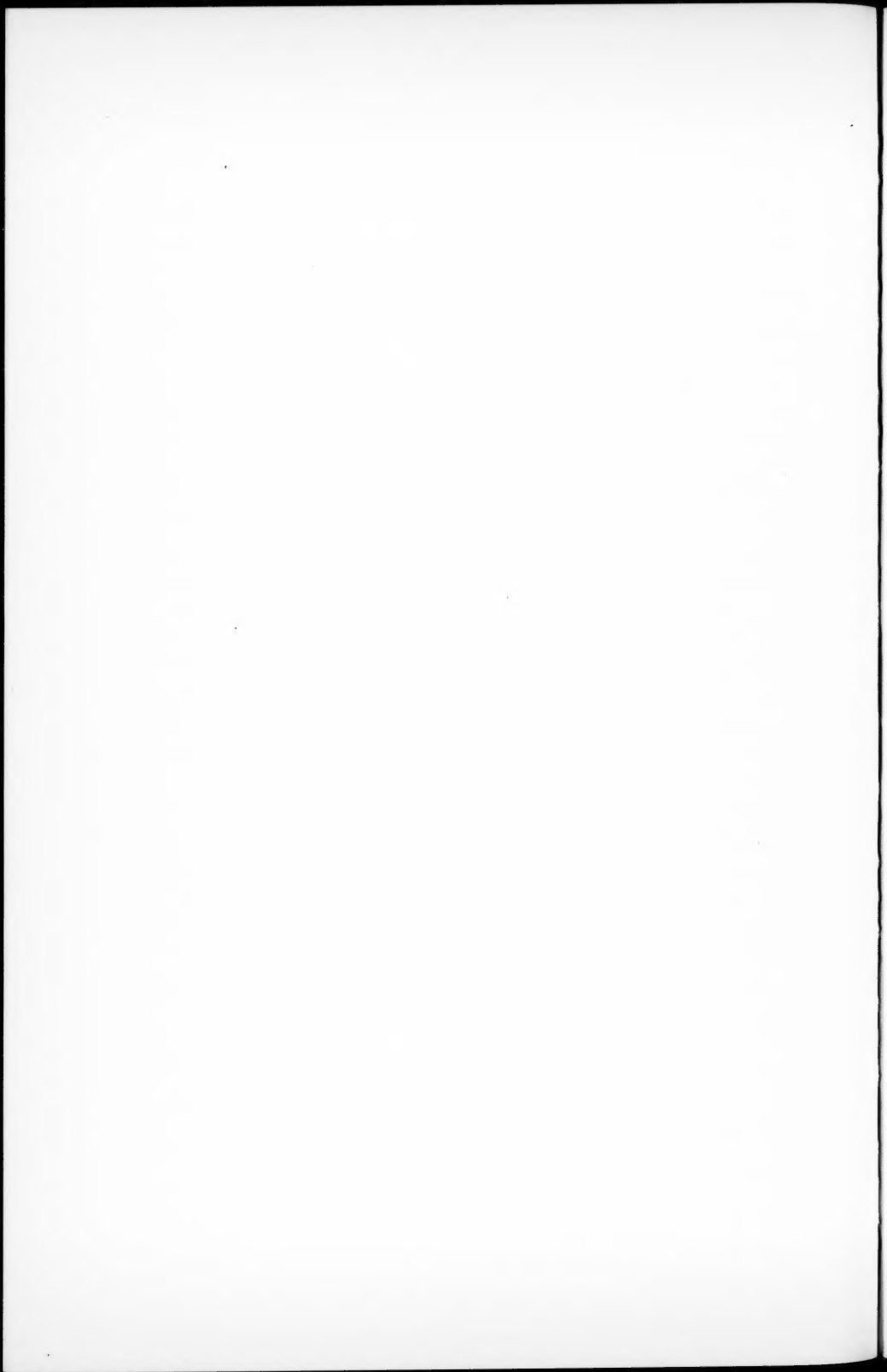
SUMMARY

There appears to be sufficient evidence that paraphilia, or the tendency to substitute reproductively non-significant sexual goals for a mate of the opposite sex, is sufficiently widespread in human populations, involves sufficiently lowered fertility and is under enough genetic control to affect the distribution of genotypes in such human populations as have been well studied. Psychoanalytic theory suggests that the most probable mode of operation of the genetic determinants is on the rates of development of neuro-psychological mechanisms involved in identification processes and other aspects of object relationship in infancy. As such, they may have pleiotropic effects of importance. A consideration of fetichism suggests that certain aspects of sexual selection in man may involve mechanisms neutralizing castration fear, and so may ultimately influence such maturation rates. The type of display involved, which seems different from ordinary epigamic display in the lower animals, is designated cryptandric.

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ONE-SIDED REPRODUCTIVE ISOLATION BETWEEN
GEOGRAPHICALLY REMOTE POPULATIONS
OF A PLANORBID SNAIL

W. LOBATO PARAENSE*

Instituto Oswaldo Cruz and Instituto Nacional de Endemias Rurais, Brazil†

INTRODUCTION

A summary of the results obtained by the author in crossing experiments between populations of hermaphroditic planorbid snails, using the recessive factor of albinism as a genetic marker, was published previously (Paraense, 1955, 1956). Matings between conspecific individuals from the same population result in the exclusive production of cross-fertilized zygotes. Even after separation of the mates, each isolated specimen continues utilizing the store of the foreign sperm, and thus produces only cross-fertilized eggs, for a time varying from about 20 days to two months or even more. Only thereafter are self-fertilized eggs laid. Results similar to those of intra-population crosses have been regularly obtained also in conspecific inter-population crosses in which the parents came from within a relatively small area (for instance, between populations about 300 kms. apart).

Some crosses of conspecific allopatric populations separated by a distance of 1,700-1,900 kms. have also been made (Paraense, 1956). Crosses readily produce fertile hybrids. "However, the events observed in these experiments were somewhat different from those recorded above when dealing with individuals from the same population. In the latter case, as stated above, cross-fertilization is steadily maintained as long as the specimens remain together. It continues also for a time after the separation of the couple, until exhaustion of the stored foreign spermatozoa. When individuals from remote populations are mated, cross-fertilization never completely replaces self-fertilization. With few exceptions, all the egg-masses from the albinos showed a mingling of pigmented and albino embryos, thus indicating some instability in the cross-fertilizing mechanism. In addition, separation of the couple is followed by a relatively speedy disappearance of the pigmented embryos, owing perhaps to a rapid exhaustion or incapacitation of the stored foreign spermatozoa. These results indicate, in a rather unique way, a lowered fertility between allopatric conspecific populations of *A. glabratus* as a result of geographic isolation.... It is interesting to note how self-fertilization makes up for the deficiency in the mechanism of cross-fertilization." (Paraense, 1956, pp. 405-406).

Further experiments have confirmed the previously obtained results, and have yielded additional data, some of which are presented below.

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†Mailing address: Caixa Postal 2113, Belo Horizonte, Minas Gerais, Brazil.

MATERIAL AND METHODS

The planorbid snail, *Taphius* (= *Australorbis*) *glabratus* (Say, 1818), was used in the following experiments. Its known present distribution covers a wide range in the Neotropical region: West Indies, Venezuela, Guianas and Brazil. Data on its morphology and taxonomy may be found in Paraense and Deslandes (1955, 1956) and Paraense (1958).

We have found that the results of crossing experiments may be misleading unless the snails crossed reproduce strictly by selfing up to the moment of being mated. If, for instance, a self-fertilizing albino is mated to an already cross-fertilized pigmented snail of its own population, the former may give a mixed (crossed and selfed) offspring, as in the above-mentioned crosses between distant populations. For this reason, we used snails grown in isolation since hatching. The experimental animals were chosen among those which had begun egg-laying about 20 days previously, and which showed a tendency to lay daily egg-clusters with gradually increasing numbers of eggs.

Ten couples were used in each crossing experiment. Each couple consisted of an albino and a homozygous pigmented individual, kept together for 20 days. After this mating period, the two snails were separated and observed for some additional period. The egg-clusters, laid on the underside of floating leaves (*Pistia stratiotes*), were collected each morning and transferred to small Petri dishes with spring water for subsequent examination under a stereoscopic microscope. The embryos were observed and scored for their pigmented or albino character, indicated by the presence or absence of the eye-spots. As albinism is recessive, the occurrence of crossing in the albino mates was ascertained merely by inspection of their F_1 offspring. As to the pigmented mates, the eggs of which always develop into pigmented embryos, the occurrence of crossing was ascertained by the segregation of the factors for pigmentation and albinism in the F_2 generation. So, the results of a single cross between a pair of snails correspond to those of reciprocal crosses between dioecious organisms. That is, each snail fertilizes its mate and is also fertilized by it. As the conclusions to be drawn from these experiments are based on the eggs produced by each mate, it was found advisable, for the sake of simplicity, to treat each mate separately as a female in relation to the other member of the couple.

Eight backcrosses were made between F_1 hybrids and specimens from the parental populations. As in the previous experiments, each couple was kept together for 20 days and then separated.

MATINGS BETWEEN SANTA LUZIA (ALBINO) AND CAPANEMA-CARACAS (PIGMENTED) STRAINS

In a first experiment, ten crosses were made between albino specimens from Santa Luzia, State of Minas Gerais, and pigmented ones from Capanema, State of Pará, localities separated by a distance of about 2,100 kms. Owing to a small difference in albumen color, the eggs of the snails from each population could be distinguished during the mating period.

A second crossing experiment was made between albino specimens from Santa Luzia and pigmented ones from Caracas, Venezuela. These two localities are about 4,100 kms. apart. As in the preceding case, a difference in albumen color permitted distinguishing the eggs from each kind of snails.

Owing to accidental contamination of the spring water, used to supply the aquaria, by a substance somewhat deleterious to the young snails, it was not possible to ascertain the normal survival rates of the F_1 s from these two crossing experiments. However, a reasonably large number of them survived up to egg-laying age and produced fertile offspring.

Albino Snails Acting as Females

1. *Capanema* \times *Santa Luzia*. The eggs laid by the albinos on the day following mating were still self-fertilized, giving only albino embryos. On the second day, the albinos of four couples laid mixtures of selfed and crossed eggs, which developed into albino and pigmented embryos respectively. On the fourth day, all the albinos of the remaining six couples were also laying selfed and crossed eggs.

The proportion of crossed eggs gradually increased in the albinos' egg-clusters. In eight cases, selfed eggs were no longer produced after the 11th day. In the two remaining cases, however, selfed and crossed eggs were always present in each cluster for the whole mating period.

On the other hand, after the appearance of the first crossed eggs in the offspring of the albinos, the numbers of eggs in their egg-clusters gradually decreased, so that, at the end of the 20-day mating period, only one or two eggs were being laid daily. In four cases, the albinos stopped laying any eggs at all, discharging only egg-cluster envelopes, either empty, or containing a number of small albumen droplets.

After separation of the mates, there was a gradual recovery of the egg-laying, both in regularity and in increase of egg numbers toward normal levels. Of the first eggs laid after separation by eight albinos, only a small number (from one to seven) were cross-fertilized; after two to 11 days, all of them turned exclusively to selfing. The two above-mentioned snails, which produced both selfed and crossed offspring during the whole mating period, did not lay any crossed egg after separation.

The following data, from the record of a mating, show the daily sequence of the observations on the offspring of an albino, beginning on the day after mating. The figures refer to the number of eggs, (0) indicating that no eggs were laid. The letters mean: (S) self-fertilized, egg developing into albino embryo, (C) cross-fertilized, egg developing into pigmented embryo, (I) inviable, development stopped before eye formation, (E) empty mass, without eggs:

15 S, 11/9 S/2 C, 7 S, 11/18 S, 11/3 C, 15 S/1 C, 5 S, 11/2 C, 4 S, 21/5 C/4 C/4 C/2 C/2 C/0/0/1 I/E/2 C/E/1 C/E, separated from pigmented mate/11/1 C/11/E/E/0/3 S, 11/5 S, 11/16 S, 21/22 S, 11/25 S/16 S/35 S/29 S, 11/30 S, 21/39 S, 11/etc.

The total number of eggs laid by the albinos of the ten couples during the mating period (recorded from the first appearance of pigmented embryos indicating actual crossing) was 751, of which 268 were crossed, 351 selfed and 132 inviable. After separation from their pigmented mates, the same albinos laid, before returning to complete selfing, 49 eggs: 25 crossed, eight selfed and 16 inviable. Thus, the total number of hybrids produced by the ten albinos in the present experiment was 293.

2. *Caracas* \times *Santa Luzia*. Contrasting with the previous experiment, in which 268 hybrids were produced by the ten albinos during the mating period, in the present one only three hybrids were produced, under similar conditions, by three out of ten snails. The numbers of eggs in the egg-clusters rapidly decreased from about the middle of the mating period, and when the mates were separated all the albinos were laying almost exclusively masses without eggs.

As in the first experiment, egg-laying gradually returned to normal after separation of the mates. Only two hybrids were produced in the post-mating period. They developed from eggs laid on the sixth day after separation, and one of them came from a snail which had already given a hybrid during the mating period. Thus, the total number of hybrids in this experiment was only five. It is interesting to note that they were produced by four albinos, and that the albinos from the remaining six couples were not cross-fertilized at all.

After having reached a high daily production of eggs, the ten albinos were placed together again with their respective pigmented mates. A decrease in the egg production ensued again, exactly as in the previous instances. Ten additional hybrids were produced during this second mating period: one by a not previously cross-fertilized snail, eight by a snail which had already produced a hybrid in the first mating, and one by the above-mentioned specimen which had produced two hybrids.

After separation of the mates, the egg-laying gradually returned to normal. In the second post-mating period only two hybrids were produced, by two different snails.

Pigmented Snails Acting as Females

The behavior of the pigmented snails in the two experiments was quite different from that of their albino mates. Not only was no decrease in egg numbers observed, but also no qualitative changes occurred in the egg-clusters.

On the day after separation of the mates, and each tenth day through the post-mating period, the egg-clusters laid by the pigmented snails of five couples from each experiment were collected. These egg-clusters were kept separately, and their respective young were grown in isolation up to egg-laying age, to determine whether they had been produced by crossing or by selfing. In the former case, the segregation of the factors for pigmentation and albinism occurred in the F_2 generation, whereas in the latter case all

the embryos were pigmented. For this test, 50 eggs from each surviving F_1 snail were examined.

1. *Capanema* \times *Santa Luzia*. All the survivors from the eggs laid by the five pigmented specimens on the first and tenth day of the post-mating period were hybrids. On the 20th day all the egg-masses contained some selfed eggs among crossed ones, and the proportion of the former increased through the remaining days. On the 40th day one specimen had stopped crossing. The other four also turned later to selfing, so that crossed eggs were no longer produced by any specimen on the 70th day.

2. *Caracas* \times *Santa Luzia*. All the survivors from the eggs laid on the first day of the post-mating period were hybrids. Subsequently, one of the five pigmented specimens turned rapidly to selfing, as in the case of the albinos, producing only pigmented offspring from the tenth day on.

Cross-fertilization lasted longer in the four remaining specimens. One of them produced crossed eggs until the 20th day and died some days later. On the 30th day, two specimens produced a few selfed eggs among crossed ones. The proportion of the former increased in the following days, so that crossed eggs were no longer produced from the 60th and 70th day on, respectively. The last pigmented specimen produced exclusively crossed offspring until the 70th day, when observation was discontinued.

It is interesting to note that the two snails which were able to keep up cross-fertilization for the longest time were just those unable to fertilize their albino mates.

BACKCROSSES

Eight matings were made in the following combinations, each of which included two couples:

1. Albino from *Santa Luzia* crossed to hybrid from *Capanema* \times *Santa Luzia*.

2. Pigmented (homozygote) from *Capanema* crossed to hybrid from *Capanema* \times *Santa Luzia*.

3. Albino from *Santa Luzia* crossed to hybrid from *Caracas* \times *Santa Luzia*.

4. Pigmented (homozygote) from *Caracas* crossed to hybrid from *Caracas* \times *Santa Luzia*.

During the whole period of observation, no quantitative or qualitative changes occurred in the eggs of any mates.

Combinations 1 and 3

The results of these matings showed that there was mutual insemination in the four couples. The ratio between pigmented and albino embryos produced by every mate was about 1 : 1 in the first five days of the post-mating period. On the following days, however, owing to the progressive diminution of the stored foreign sperm, the proportion of selfed embryos gradually increased, leading to the eventual production of only albinos by the albino parents, and of three pigmented to one albino by the hybrid parents. The

stabilization of the ratios between pigmented and albino embryos at the 3:1 and 0:1 levels, indicating exclusive self-fertilization in the hybrid and albino parents, respectively, took place between the 30th to the 60th day of the post-mating period.

Combinations 2 and 4

As in the combinations 1 and 3, the four hybrids were fertilized by their homozygous mates. Shortly after having been separated from the latter, the hybrids produced some albino embryos, indicative of selfing. The albinos gradually increased in relative numbers on the following days, until becoming eventually stabilized around the Mendelian ratio of 3:1 from the 20th to the 50th day of the post-mating period. Cross-fertilization lasted longer (40' and 50 days) in the two hybrids between Capanema and Santa Luzia than in the others (20 and 35 days).

The data from the pigmented homozygotes (F_2 generation) are still incomplete and will not be presented here.

DISCUSSION

In our preceding paper (Paraense, 1956), results of intrapopulational and interpopulational crosses in *T. glabratus* were recorded, showing that, as the distance between the populations increased, a gradual decrease in interfertility became apparent. The present experiments bring a confirmation of those results, showing even lower degrees of interfertility clearly correlated with the increased distance between the populations. However, in the present experiments (and in all probability also in the preceding ones), such an interpretation holds good only as regards the albino mates acting as females.

As far as the albinos are concerned, the most noticeable aspects of the present experiments are the gradual diminution in the daily number of eggs and the comparatively small number of hybrids produced by them through the mating period.

The lowered hybrid production was regarded, in the preceding paper, as a result of the failure of the foreign spermatozoa to fertilize all the available eggs. "It seems evident that the partial intersterility depends in these cases on a certain degree of gametic isolation. This isolation is caused perhaps by some deleterious effects of the genitalic secretions, or by some other biochemical response against foreign spermatozoa." (Paraense, 1956, p. 406). In the present experiments the partial intersterility was even more pronounced, no hybrids having developed from the eggs of some albinos in the matings between the most remote populations (Caracas \times Santa Luzia).

The diminution in the number of eggs through the mating period had not been observed in previous experiments with less distant populations. This may be regarded as a result of an intensification of the "biochemical response against the foreign spermatozoa," postulated in the preceding paper. That such a lowered individual fertility depends on previous copulation may be inferred from the facts that it followed the appearance of the first cross-

fertilized eggs (in the first experiment), ceased after the separation of the mates, and recurred again after a new mating.

At the end of the mating period, the diminution in egg numbers attained its extreme degree in the deposition of jelly-like masses containing all the components of an egg-cluster except the egg-cells themselves. One of these masses is shown in figure 1, in comparison with a normal one.

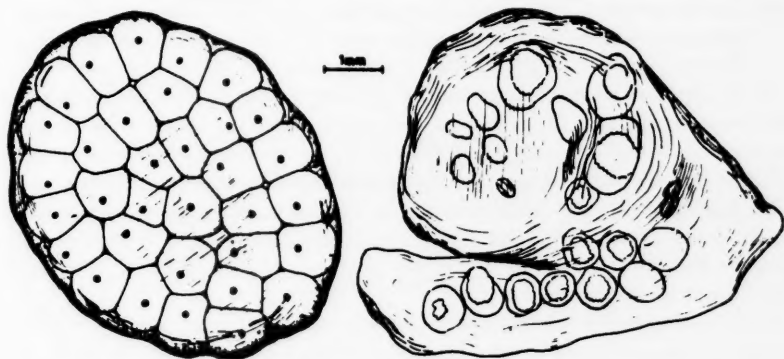


FIGURE 1. Left: normal egg-mass of *T. glabratus*. Right: defective mass, without egg-cells, laid by albino specimen from Santa Luzia crossed with pigmented specimen from Capanema.

A normal egg-cluster is formed by a number of spherical capsules filled with albumen, each of which usually contains a single fertilized egg. A group of such capsules is cemented by a jelly-like substance, and the whole is enveloped by an outer membrane. The eggs, formed in the ovotestis, travel down the hermaphrodite duct and are passed, most probably already fertilized, into the so-called carrefour. The latter is a bulbous swelling, into which the secretion of the albumen gland empties, and from which arise the male and female ducts. Each egg is surrounded by a drop of albumen in the carrefour, then is encapsulated, descends the oviduct and is clustered together with others in the nidamental gland, to be deposited through the vaginal opening. Since the only missing components of the above-mentioned abnormal formations are the egg-cells, it is reasonable to suppose that their absence should be ascribed to some hindrance arising above the carrefour, probably at some point of the hermaphrodite duct. Similar defective masses have been observed laid by snails infected in our laboratory with larval stages of the trematode, *Halipegus dubius* Klein. After a period of normal egg-laying, the passage of egg-cells was suppressed, and the anatomical examination of the snails showed a break in the hermaphrodite duct resulting from the destruction of its extremely thin wall by the trematode rediae.

Work to obtain information on the cause of the changes associated with the aforementioned type of isolating mechanism is in progress. It seems not

improbable that something analogous to the "insemination reaction" described by Patterson (1946) in *Drosophila* may be in operation.

It might be supposed that the changes in the reproductive behavior of the albinos would depend on some kind of pleiotropic effect from the factor of albinism. Even in this case, however, such changes cannot be dissociated from the geographic factor, as they increase in proportion to the distance between the populations. If they depended on albinism only, they would also occur in the albinos crossed with pigmented specimens from nearer populations. Additional investigation on this particular subject is being carried out.

With regard to the pigmented snails, we were surprised by the high degree of cross-fertilization of their eggs, contrasting with the lowered production of cross-fertilized eggs by the albinos. In our previous experiments with less remote populations, we took for granted that the inferences drawn from the observation of the albinos might be applied to their pigmented mates. In the present experiments, however, the absence of changes in egg-production by the latter led us to investigate the composition of their offspring, with the results described above.

A kind of reproductive isolation somewhat related to that observed in the present study seems to be that referred to by Dobzhansky (1951, p. 187), in species of *Drosophila*, as "one-sided sexual preference." However, although it may be supposed that the evolutionary significance of both kinds of isolating mechanisms does not differ substantially, their physiological bases certainly do.

Owing to the above-mentioned disturbing effect of water contamination on some batches of young F_1 snails, and to the small number of backcrosses in each combination, no conclusions are drawn with respect to some questions concerning the hybrids, such as survival rates, degrees of fertility and compatibility, and others, which will be dealt with in another study. Nevertheless, the results obtained here are sufficient to reveal a noticeable degree of compatibility of the genotypes concerned, which leads to the disappearance, in the backcrosses, of the more remarkable changes in egg and hybrid production observed in the parental crosses.

SUMMARY

Crossing experiments were made between remote populations of the planorbid snail, *Taphius glabratus*, using albinism as a genetic marker. Each couple consisted of a recessive albino from Santa Luzia, Brazil, and a homozygous pigmented specimen from either Capanema, Brazil (2,100 kms. from Santa Luzia), or Caracas, Venezuela (4,100 kms. from Santa Luzia).

After copulation, egg production by the albinos decreased until abnormal masses without eggs were eventually deposited. These abnormalities were most intense in the matings between the most remote populations. Cross-fertilized eggs from albinos were much less numerous in the matings Capanema \times Santa Luzia than in those between populations from less remote lo-

calities. They were even less numerous in the matings Caracas \times Santa Luzia, in which some albinos produced no cross-fertilized eggs at all.

Egg production by the pigmented specimens remained unaffected after copulation. Moreover, cross-fertilized eggs were laid by them in much greater numbers than by the albinos.

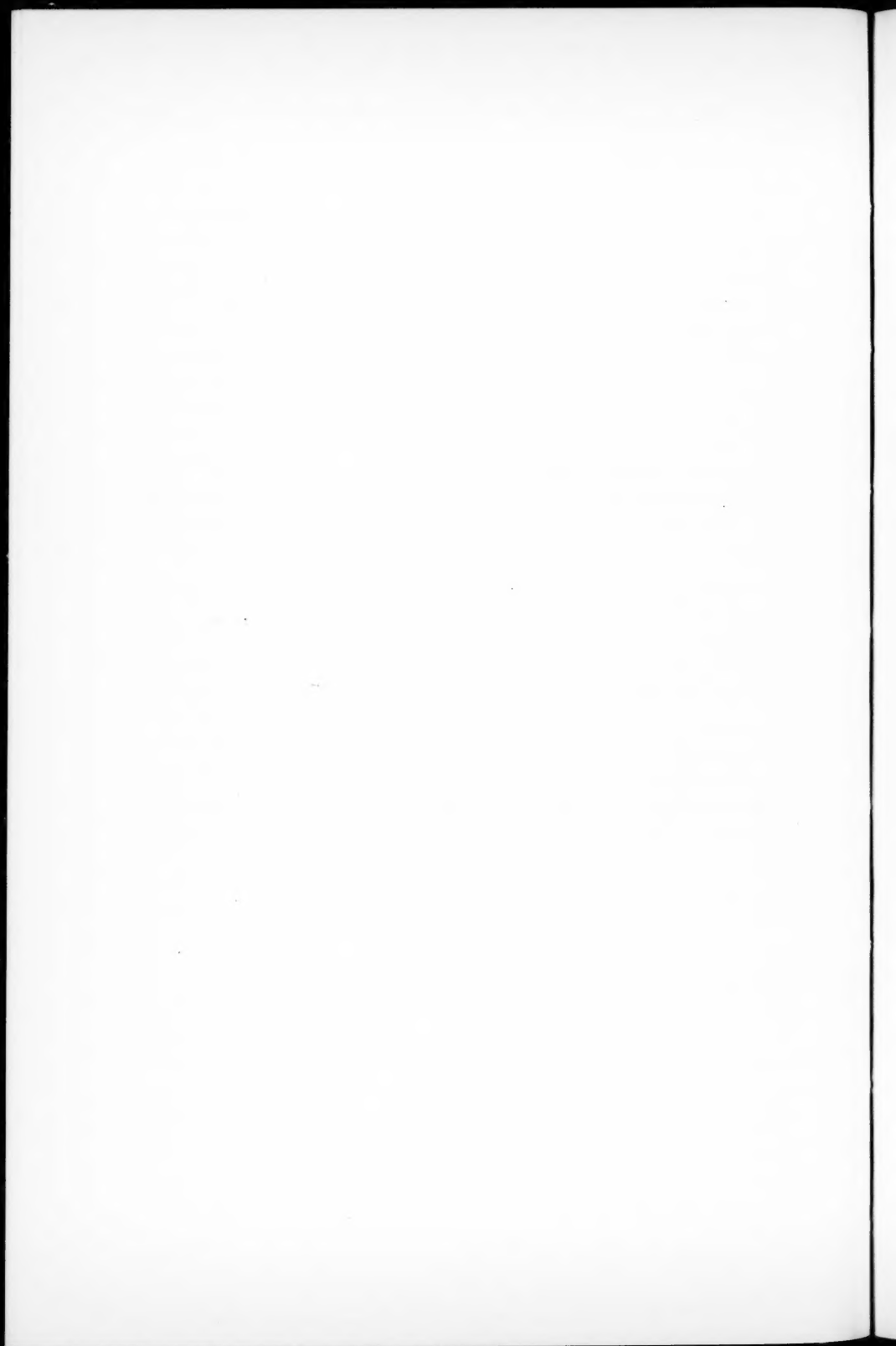
If the sexes of these hermaphrodite snails are considered separately, it will be seen that there are definite degrees of reproductive isolation, associated with geographical distance, between northern males and southern females. The same is not true for southern males and northern females. In this case, only a slight degree of reproductive isolation is suggested by the comparatively rapid exhaustion of the stored foreign sperm in some specimens.

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A GENERAL EVOLUTIONARY PRINCIPLE UNDERLYING THE ORIGIN OF DEVELOPMENTAL HOMEOSTASIS

R. L. BERG

Department of Darwinism, Leningrad State University, Leningrad, U.S.S.R.

The purpose of the present note is to suggest the possible evolutionary factors which underly the origin of developmental homeostasis. Relative independence of certain characteristics of form and function from environmental variations is taken as an indication of homeostatic buffering. A comparative study has been made of variation in nineteen plant species. Various characteristics of the same species often differ in the degree of their stability (or variability), and the variations in these characteristics may be to some extent correlated or more or less independent. An attempt has been made to relate the stability or variability of the characters to their adaptive functions, and to infer from this relation the ecological mechanisms which lead to the origin of higher degrees of developmental stability (Berg, 1958).

The characters studied were dimensions of certain parts in the nineteen species selected for this purpose. The degree of stability can be expressed as a ratio of the maximal and the minimal values attained, or as the variation coefficient. The greater the stability of the dimensions of the part under consideration, the smaller is the maximum: minimum ratio and the coefficient of variation. Conversely, lesser stabilities make these values greater. The degree of the independence of characters is indicated by weakness or by lack of correlation between them. The higher the correlation observed between the dimensions of two parts, the less is the degree of their independence from each other.

The plant species used as materials for the present study can be divided into four groups, according to the characteristics of their flowers. Some are self-pollinated, or wind-pollinated, or pollinated by unspecialized insects, while others are pollinated by specialized insects. Some have symmetrical and others zygomorphic flowers. These four groups are as follows:

Group	Species	Characteristics of the flowers
I	<i>Triticum aestivum</i> <i>Hordeum vulgare</i> (2 varieties) <i>Elymus arenarius</i> <i>Anemone nemorosa</i> <i>Papaver</i> sp. <i>Fragaria collina</i> <i>Cosmos bipinnata</i>	Self-pollinated, wind-pollinated, or pollinated by unspecialized insects
II	<i>Geranium pratense</i> <i>Chamaenerium angustifolium</i>	Radial flowers, laterally placed, having no tubular parts, pollinated by specialized insects.

Group	Species	Characteristics of the flowers
III	<i>Lychnis viscaria</i> <i>L. chalconica</i> <i>Melandrium sylvestre</i>	Radial flowers, with tubular parts, having specialized insect pollinators
IV	<i>Delphinium elatum</i> <i>Linaria vulgaris</i> <i>Digitalis ambigua</i> <i>D. purpurea</i> <i>Tropaeolum majus</i> <i>Nicotiana glauca</i> <i>Phlox divaricata</i>	Dorsiventral laterally placed flowers, with tubular parts, or the entire corolla transformed into a tube (<i>Digitalis</i>), pollinated by specialized insects

The plant parts studied were classified into vegetative and reproductive according to the specific significance of their form and dimensions for the process of reproduction. Stems, leaves and inflorescences are vegetative parts; stamens, pistils, corolla and calyx are reproductive parts. Some parts of the flower act as distance signals for the pollinating insects (laminal parts of the perianth), others help to deposit the pollen on some definite part of the pollinating insect's body (the tubular parts of the perianth and the stamen filaments). The process of the deposition of the pollen on some definite part of the body of a specialized pollinating insect was first described by Darwin in Orchidaceae and recently by Schwanvitsch in Papilionaceae. The structure of some flowers, the pollen of which is transferred by specialized pollinating insects, is adapted for each deposition of the pollen on a definite part of the body of the pollinating insect.

In all the species studied the dimensions of stems, leaves and inflorescences, that is, the dimensions of vegetative parts, have a much greater range of variation as compared with the reproductive parts. With very few exceptions, the dimensions of all these parts in all the species studied are correlated with one another. In the seven species of the first group, high positive correlations were found to exist between the dimensions of all the parts studied, including the reproductive parts. No exceptions were observed.

In the twelve species belonging to the second, third and fourth groups, that is, in the species possessing specific pollinators, no correlation between the dimension of vegetative and reproductive parts was observed, irrespective of the type of floral symmetry, of the position of the flower on the plant, and of the presence or absence of tubular parts in the flowers. The few exceptions are found mostly in ornamental plants.

In the ten species of plants possessing tubular flowers, it is actually the size of the tubes that shows the smallest range of variation, the smallest variation coefficient, and absence of correlation with the dimensions of the vegetative parts of the plant. A high positive correlation was observed between the dimensions of the reproductive parts, although exceptions were not rare.

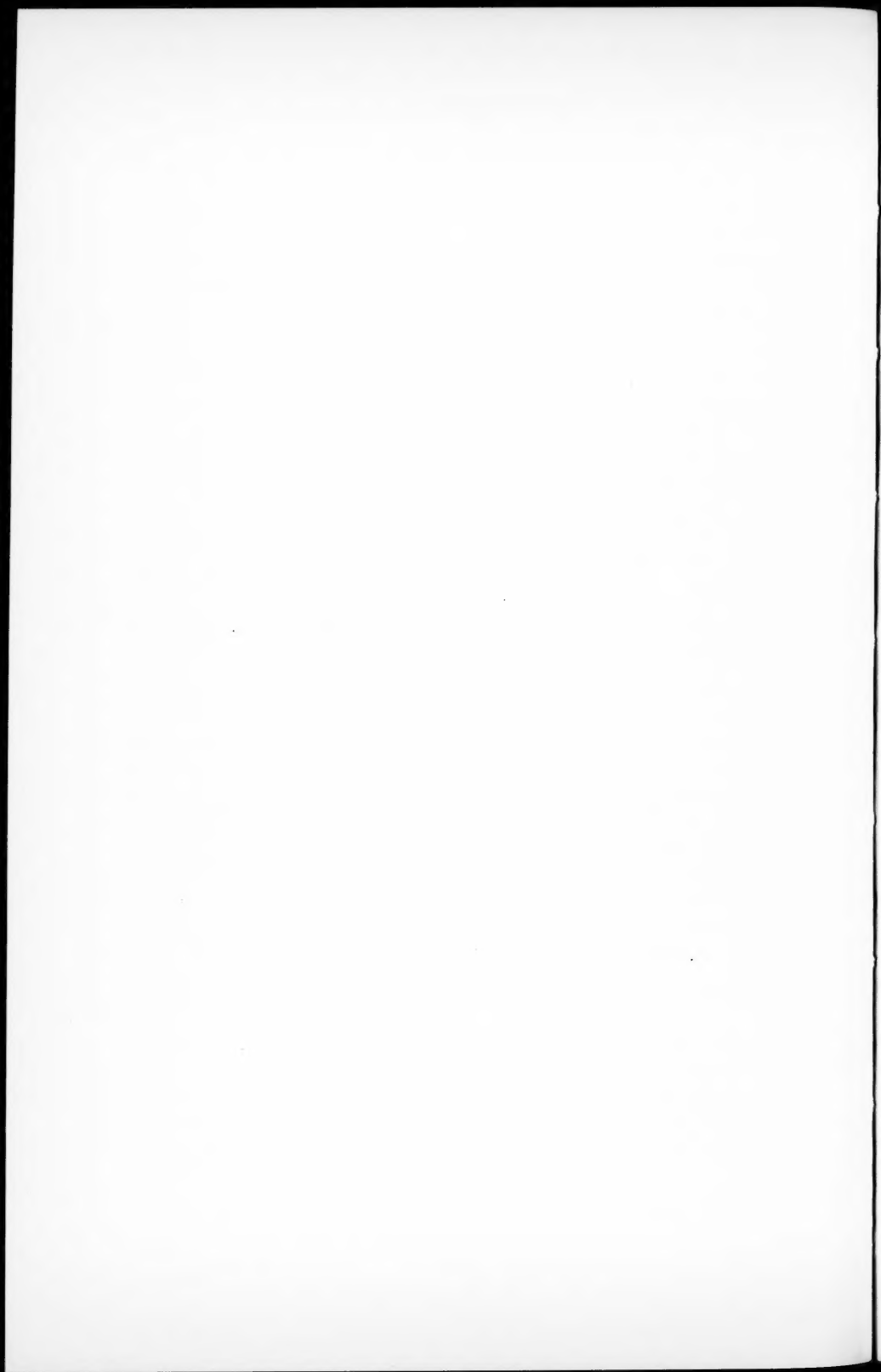
The part of the flowers specialized to deposit the pollen on a definite point of the body of the pollinating insect are most interesting for our purpose. Such parts show a remarkable stability of their dimensions within a

species, and also lack of correlation with the dimensions of other body parts of the same individual plant. The biological function of the adaptations to localize the pollen deposit on some definite part of the body of the pollinating insect is probably to reduce the wastage of the pollen. This is especially true if the pollen is deposited in a location on the insect's body which is out of reach of its pollen-removing organs. Now, the precise localization of the pollen deposit is functionally effective only if the flowers of the species have all approximately equal dimensions. The size of every flower must, thus, be fitted not only to the dimensions of the specialized insect pollinators, but also the flowers of different individuals in a cross-pollinating population must be rather uniform. A flower which locates its pollen on the insect's body incorrectly is likely to have no progeny. Pollinating insects act, then, as selective agents with respect to the dimensions of the floral parts. They take no part whatever in the formation of flowers in the course of ontogeny.

In higher organisms formative and selective factors rarely coincide. This lack of coincidence between the formative and the selective factors is responsible for the reinforcement of internal factors of development; the environmental factors gradually lose their influence, and at the same time developmental homeostasis arises. Homeostasis has adaptive significance in those cases where the function has no formative capacity but acts exclusively as an approval. This is just the case in the interrelation between the flowers and their specific pollinating insects with respect to the forms and dimensions of flowers. The general principle underlying the origin of homeostasis in the process of evolution is the discrepancy between the agencies participating in the formation of the character and the selective forces determining its function. In the process of evolution this principle came into action simultaneously with the origin of the alternation of generations, and acquired special importance after the origination of ontogeny. Coding inherent in the physical basis of heredity is its direct consequence.

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AN ELECTROPHORETIC STUDY OF EGG-WHITE PROTEINS IN TWENTY-THREE BREEDS OF THE DOMESTIC FOWL

CHARLES G. SIBLEY AND PAUL A. JOHNSGARD

Department of Conservation, Cornell University, Ithaca, New York

INTRODUCTION

A "conservative" taxonomic character is one which preserves evidence of evolutionary relationships. As Mayr (1942: 296) points out such characters are rare because structures are usually lost quickly when no longer needed and selection seldom neglects a functional structure for very long but continually modifies it as adaptive fitness is increased. However, because different characters evolve at different rates it is possible to find some characters which have changed more slowly than others and to use these as phylogenetic indicators. In birds, for example, plumage color and structure apparently change more rapidly than the skeleton or the muscular system. This is demonstrated by studies such as that of Hudson and Lanzilotti (1955) on the wing muscles of the Corvidae. In 19 species representing 14 genera of crows, nutcrackers, magpies and jays the wing musculature showed "remarkable uniformity" and the small differences noted did "not suggest any taxonomic groupings." The wing musculature in this instance was a conservative family level character which had not been basically modified during the evolutionary changes involved in the proliferation of the species which were studied.

Under domestication it is possible to accelerate hereditary changes by artificial selection (Lerner, 1958). In the Domestic Fowl (*Gallus gallus*) a remarkable array of characters has been established as the traits of different "breeds," many of them within the past century or two. The various breeds range in size from tiny bantams weighing less than two pounds to large exhibition varieties weighing ten or 12 pounds. Body shapes range from the slim "game" breeds to the heavy-bodied, meat-producing types. Plumage variations in color and form are remarkable and include the continually growing central rectrices of the Phoenix Fowl. Other breeds are characterized by crests, feathered feet, "silky" plumage and other variations. The Houdan has a double hind toe and a "split" comb. The wild ancestral Jungle Fowl has a well-defined breeding period and clutch size, but some domesticated breeds lay almost continuously and have nearly lost their brooding tendencies. Breeds vary in their resistance to disease, parasites and vitamin deficiencies; in egg size, egg shape, egg color, hatchability and freedom from blood spots in the eggs (Lerner, 1958). Variations are also found in dominance tendencies and in the frequency with which the various male displays are given (Williams and McGibbon, 1955).

It seems likely that no important feature of the Domestic Fowl has remained entirely exempt from modification. If the various breeds were judged

taxonomically on a purely morphological basis they would certainly constitute many species and several genera. In this situation the search for "conservative" characters is especially difficult and only those features important for survival or which have not been singled out by artificial selection are likely to show stability.

THE EGG-WHITE PROTEINS

It might be expected that the composition of such substances as the egg white would not be affected by selection for size, color, etc., but the possibility of pleiotropic effects cannot be disregarded. In an electrophoretic study of egg-white proteins of 37 species of birds McCabe and Deutsch (1952) found no evidence of differences among several breeds of chickens, but no systematic study had been made.

Therefore, an investigation of protein composition, as determined by paper electrophoresis, was initiated.

METHODS AND MATERIALS

Fresh eggs from three hens of each of the following eight breeds were obtained: Rhode Island Red, Barred Rock, Cornish Game, Partridge Plymouth Rock, White Leghorn, Houdan, Brown Leghorn and New Hampshire Red. Total number of eggs sampled from each of these breeds ranged from 25 to 28. In addition, from one to three eggs were sampled from the Red Jungle Fowl, Light Brahma Bantam, Black-tailed Japanese Bantam, Old English Black Red Bantam, Gray Japanese Bantam, Plain Mille Fleur Bantam, Old English Spangled Bantam, Black Java, Silver Leghorn, Golden Pencilled Hamburg, Rhode Island Red Bantam, Partridge Wyandotte Bantam, Sultan, Old English Black Bantam, and Dark Cornish Bantam.

The eggs were opened at one end and a sample of the thin outer albumen was obtained by filtration through coarse cheese cloth. This technique prevented the thicker layer of albumen, which contains a higher percentage of the glycoprotein ovomucin, from entering the sample. Since ovomucin is insoluble in barbital buffer and precipitates out at the point of application, its presence only made the take-up of the sample by a micro-pipette more difficult and was therefore undesirable. The samples were placed under refrigeration until they were used.

The electrophoretic apparatus used was manufactured by the Spinco Division of Beckman Instruments, Inc., and consisted of a standard "Durrum" cell (Model R), a constant current power supply ("Duostat") and associated equipment for dyeing, rinsing and fixing the paper strips. The buffer used was the Spinco B-2, consisting of a mixture of diethyl barbituric acid and sodium diethyl barbiturate to provide a liter of solution with a pH of 8.6 and an ionic strength of 0.075. All separations were made at a constant current of eight milliamperes per cell during a period of 16 hours at room temperature.

Six microliters of thin albumen were placed on each of the eight strips (30 x 305 mm.) and following the 16 hour separation the strips were dried in

a forced air convection oven at approximately 120°C, dyed in bromophenol blue (six hours), then rinsed, fixed and dried according to the procedure specified by the manufacturer (Spinco, Procedure A).

The resulting dyed strips were analyzed by the Spinco "Analytrol" (Model RB) which "translates" the protein components into a pen-drawn curve, with the height of the curve being in direct proportion to the protein density at any given point.

RESULTS

The profiles in figure 1 represent typical curves obtained from each of the eight breeds from which 25 or more eggs were obtained. The superimposed histograms indicate the percentage of total protein found in each centimeter unit, with a scale of three per cent for each centimeter of vertical height. These percentages were obtained by means of the automatic integrator of the "Analytrol," which provides an index to the area subtended by the electrophoretic profile trace. The profiles of the other 15 breeds, from which fewer eggs were available, fall within the range of variability indicated in figure 1. Figure 2 presents the average percentage of total protein in each centimeter of the profiles of 244 eggs from all 23 breeds.

Figure 1 indicates the similarity in the electrophoretic patterns among all of the breeds sampled. All breeds show a small cathodally migrating portion, which contains the enzyme lysozyme. This component tends to move a maximum of about three centimeters from the point of application and makes up about eight per cent of the total protein profile.

A slight peak is sometimes present immediately above the point of application which indicates the presence of the insoluble ovomucin not entirely removed through filtration. A non-filtered sample would show a much higher percentage of this component, and thus its amount is not of significance in this comparison.

The first major peak is found in all cases to be at the first anodal centimeter. This is the ovoalbumin fraction. Anodal centimeter one averaged about 16 per cent of the total protein profile. Longworth *et al.* (1940) found that the ovoalbumin fraction averaged about 14 per cent of the total albumen protein (excluding ovomucin), which does not differ greatly from our results.

The second, lower anodal peak, which is found at about anodal centimeter two, represents the ovomucoid fraction. This fairly discrete component also contributes about 14 per cent of the total soluble albumen protein (Longworth *et al.*, 1940).

Between anodal centimeters three to five are found small amounts of protein which do not separate into distinct fractions. These apparently represent, in addition to "tailing" of the ovalbumin, the globulin fractions G₂ and G₃. The poor separation of these components in all the breeds studied probably resulted from an unsatisfactory pH and the resolution limitations of the filter paper medium.

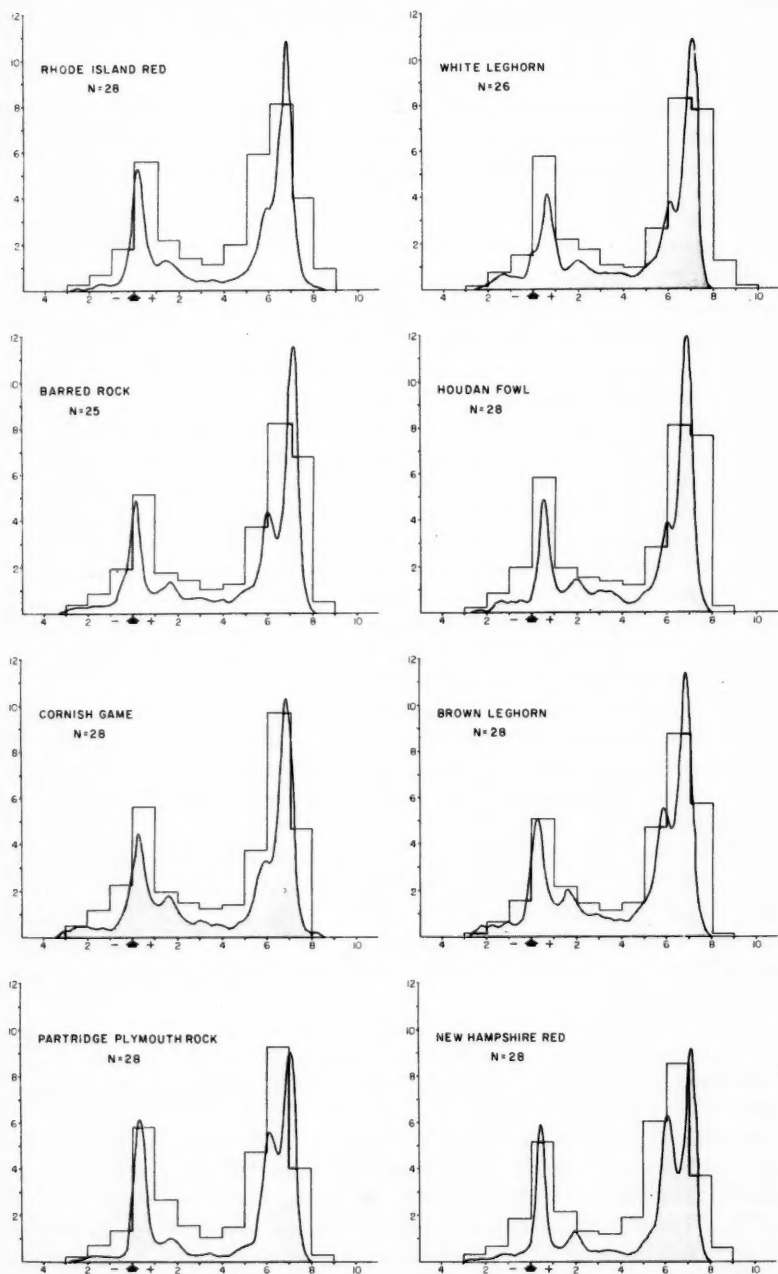


FIGURE 1. Typical electrophoretic profiles of the egg-white proteins of eight breeds of domestic fowl. The histograms indicate the percentage of total protein in centimeter units. Each centimeter on the vertical axis = 3%.

The remainder of the profile consists of the major component, ovalbumin. As the figures indicate, this is actually composed of two major portions, ovalbumin A_1 and A_2 , the latter usually appearing as a "shoulder" on the trailing edge of the major A_1 peak. Some samples independent of breed, showed a distinct tendency of the A_1 peak to separate into two components, the second appearing on the leading edge of the major peak. These variations are known to be due to differences in phosphorus content (Perlmann, 1950; 1952) and the different ovalbumins differ from one another in one or two phosphoric acid residues (Fevold, 1951; Warner, 1954).

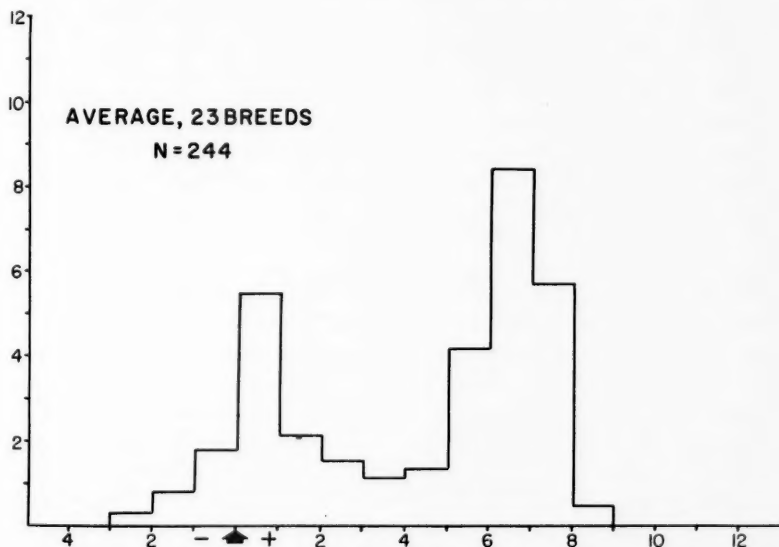


FIGURE 2. Average percentage of total protein in centimeter units for 244 eggs from 23 breeds of domestic fowl. Each centimeter on the vertical axis = 3%.

According to Longworth *et al.* (1940) the total ovalbumin fraction comprises about 60 per cent of the albumen protein. Average percentages obtained by us for the eight major breeds studied were about 57 per cent. Albumin "tailing" losses on the paper medium probably account for the slight differences found.

To provide a more precise method for comparing the major breeds studied, the average percentage of total protein per centimeter in both directions from the point of application was calculated and is presented in table 1. These data, from which the histograms were derived, indicate the generally small amount of variability found in the protein profiles of the breeds studied. Only in two places do these figures show greater variability than might be expected from sampling errors and the quantitative limitations of the technique. These are in anodal centimeters 6 and 8, where average deviations

TABLE I
AVERAGE PERCENTAGE OF TOTAL PROTEIN PER CENTIMETER

Breed	N	Centimeters from point of application													
		-4	-3	-2	-1	+1	+2	+3	+4	+5	+6	+7	+8	+9	+10
Partridge	28	.05	.78	1.98	4.04	17.41	7.68	4.74	3.16	4.28	13.93	28.11	12.45	1.26	.01
Plymouth Rock	26	.13	.57	2.04	4.34	16.94	6.91	4.79	3.11	2.72	7.59	24.74	23.23	3.53	.01
White Leghorn															
Rhode Island															
Red	28	.03	.67	2.15	5.41	16.26	6.37	4.13	3.26	5.84	17.39	24.05	11.88	2.62	.09
Barred Rock	25	.12	1.22	2.31	5.68	15.31	5.52	4.26	3.14	3.70	11.33	25.00	20.57	1.76	.00
Cornish Game	28	.09	1.30	3.17	6.67	16.71	5.84	4.40	3.73	4.02	11.04	28.78	14.54	.04	.00
Houdan	28	.00	.36	2.43	5.71	17.51	5.63	4.47	3.92	3.52	8.26	24.31	22.95	.81	.00
New Hampshire															
Red	28	.09	.60	1.70	5.42	15.46	6.55	3.90	3.65	5.77	18.21	25.49	11.22	1.88	.00
Brown Leghorn	28	.00	.43	2.05	4.72	15.35	6.81	4.62	3.63	4.77	13.97	26.43	17.17	.38	.00
Ave., 8 breeds	219	.06	.74	2.23	5.25	16.37	6.32	4.41	3.45	4.29	12.71	25.86	16.75	1.53	.01
Ave. Deviation															
8 breeds	219	.04	.36	.31	.66	.77	.53	.23	.27	.80	3.16	1.43	4.22	.91	.02
Ave., 23 breeds	244	.06	.75	2.25	5.25	16.26	6.35	4.45	3.48	4.24	12.45	25.92	17.13	1.40	.01
Ave. Deviation															
23 breeds	244	.04	.26	.30	.59	.81	.48	.26	.26	.76	3.15	1.32	4.26	.91	.02

from the mean combined breed profile are approximately three and four per cent. This results from the fact that these points represent the leading and trailing edges of the major ovalbumin fraction, and minor variations in the total distance moved by this fraction greatly affect the amount of protein to be found in these two centimeter units. Thus the percentage protein for centimeter six tends to be high in some breeds (Rhode Island Red, New Hampshire Red) and correspondingly low in centimeter eight, or the reverse situation may obtain as in the White Leghorn and Houdan Fowl.

DISCUSSION AND CONCLUSIONS

The variation encountered in the egg-white proteins of the 23 breeds studied was no greater than can be explained on the basis of individual variation and sampling and measuring errors, and is not correlated in any observable way with breed differences. The variations are no greater than one would obtain in the measurement of the classical anatomical features of plumage, size and shape of body and skeleton, or other features usually used by taxonomists in characterizing a species. In this regard, the egg-white proteins show the same stability which Yamashina (1944) found in chromosome number and morphology of 17 varieties of Domestic Fowl. Thus selection for external morphological characters does not necessarily affect the basic protein structure, and evidence of phylogenetic relationships may be conserved in the proteins after it has been obscured in more superficial characters by the effects of selection for "signal" characters or other functions.

The electrophoretic profiles of the egg-white proteins of more than 360 species of birds have been studied up to November, 1958, including some 30 species of the family Phasianidae which includes the Domestic Fowl (Sibley, in press). The similarity in pattern which extends through groups of related species is striking and further indicates the phylogenetic conservatism of the egg-white proteins. For example, the profiles of the Turkey (*Meleagris gallopavo*) and Ring-necked Pheasant (*Phasianus colchicus*) are similar to that of the Domestic Fowl. These three species, although considered on morphological grounds to represent three separate genera, show a high degree of interfertility. Hybrids between *Gallus* and *Phasianus* are not uncommon and *Meleagris* × *Phasianus* hybrids have been produced by Asmundson and Lorenz (1955, 1957). *Meleagris* × *Gallus* hybrids have not yet been brought to hatching although fertility is fairly high and 22-day embryos have been obtained. Sokolow *et al.* (1936) have reported that the chromosomes of the Turkey and Ring-necked Pheasant are more alike than those of the Pheasant and Domestic Fowl. All of these lines of evidence suggest a closer relationship among these three species than is indicated by external morphology. Exactly parallel cases are found in the ducks of the genus *Anas* and doves of the genus *Streptopelia*.

The evolutionary conservatism of proteins has also been demonstrated at the most fundamental structural level by the important work of Sanger and his colleagues (Brown, Sanger and Kitai, 1955; Harris, Sanger and Naughton,

1956) in their studies of the amino acid sequence in the insulin molecule. The insulins of five mammalian species have been worked out and such differences as exist are all located in one small segment of the molecule. In commenting on the taxonomic value of proteins Crick (1958) suggests that the structure of these molecules may contain "the most delicate expression possible of the phenotype of an organism and that vast amounts of evolutionary information may be hidden away within them."

SUMMARY

Fresh albumen samples from a total of 244 eggs from 23 breeds of Domestic Fowl (*Gallus gallus*) were analyzed electrophoretically. These breeds include the wild-type Red Jungle Fowl, as well as a wide variety of bantam, laying, and exhibition breeds which provide a large amount of morphological and physiological diversity. No variation in the egg-white proteins among these breeds could be detected that was greater than normal sampling and measuring errors inherent in the technique. It is concluded that the structure of the egg-white proteins is phylogenetically conservative.

ACKNOWLEDGMENTS

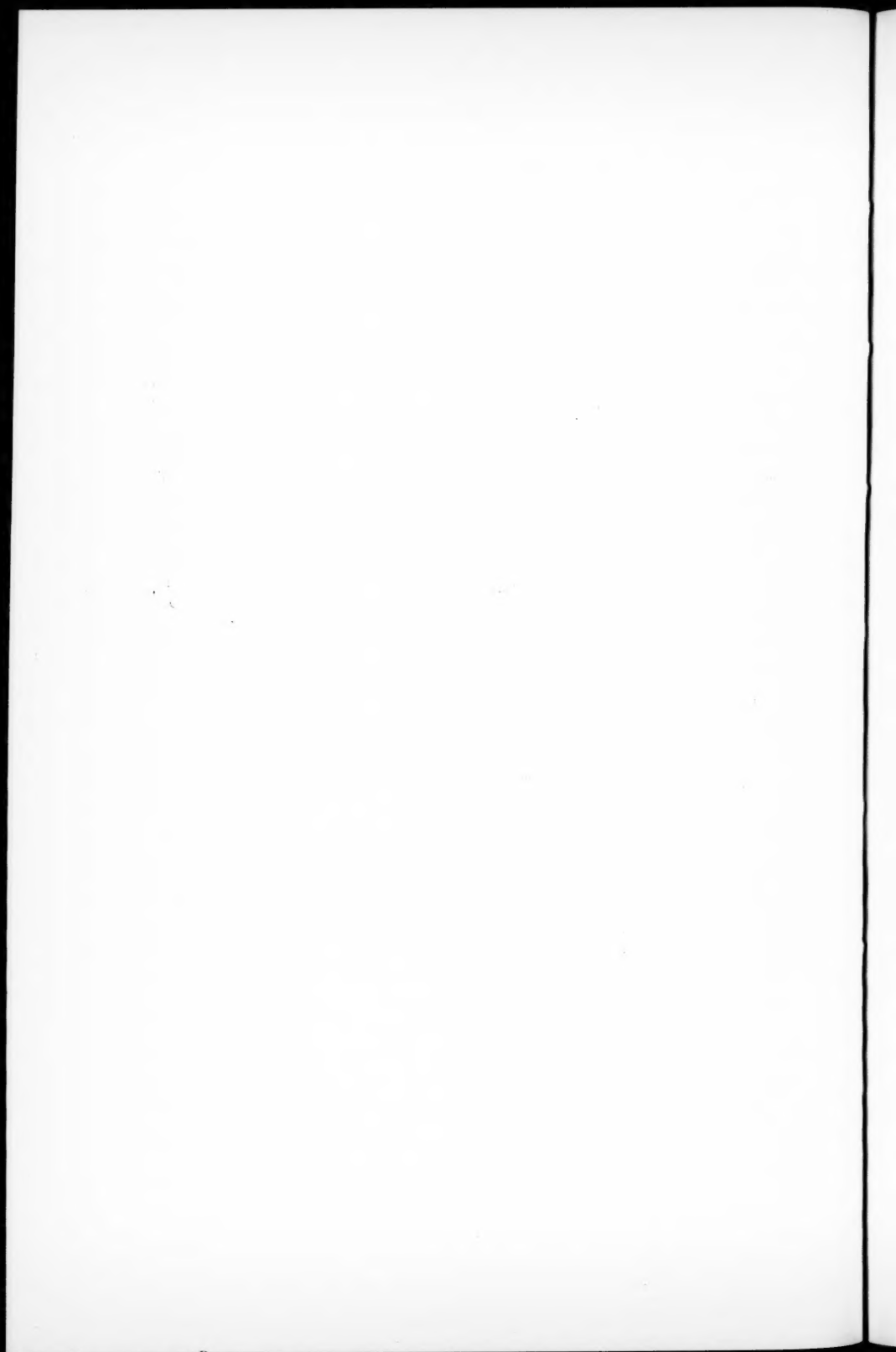
We are indebted for assistance with the laboratory work to Miss Philippa Claude. The National Science Foundation has supported this work (NSF G-1832 and G-4562), and the New York State College of Agriculture at Cornell University has provided facilities and equipment.

We are grateful to the Cornell University Department of Poultry Husbandry which provided the eggs of the first eight breeds listed and to Mrs. Florence Ray of Horseheads, New York, who provided the eggs of the other 15 breeds.

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A THEORETICAL ECOLOGICAL MODEL OF SIZE DISTRIBUTIONS
AMONG SPECIES OF ANIMALS

G. E. HUTCHINSON AND ROBERT H. MacARTHUR

Osborn Zoological Laboratory, Yale University, New Haven, Connecticut.
Edward Grey Institute of Field Ornithology, Oxford University,
England, and Division of Biology, University of
Pennsylvania, Philadelphia, Pennsylvania

If we examine the fauna of any area we find that the groups containing the largest numbers of species are for the most part groups of small animals, whereas large animals are represented mainly by genera containing a few species. This is in part doubtless an expression of the Eltonian pyramid of numbers and sizes; there will usually be few species of groups in which there are few individuals, so that rare, large carnivores, high in the pyramid, are unlikely to show much specific diversity. This however cannot be the sole explanation; in any fauna the carabid beetles for instance are likely to be richer in species than the carnivorous mammals and birds, while the largest terrestrial animals are herbivorous mammals in practically all non-insular undisturbed faunas. It would seem intuitively that the environment does not provide adequate room for a very large number of species of large animals while there is much more room for an abundance of smaller species. Moreover it is quite obvious in many cases that the large species roam about over a number of biotopes specific for smaller species. A large ungulate may require a water hole, a grazing area and some degree of cover; the wet marginal area of the water hole, the open grazing area and the cover might provide specific biotopes for three species of rodents.

In order to clarify somewhat these ideas, the following model has been developed.

STATEMENT OF THEORY

Consider an environment composed of an indefinite number of equal-sized mosaic elements of r different kinds arranged in a random way. Select from this environment n contiguous elements. In any selection there will be x kinds of elements where x can have the values $1, 2, \dots, n$ (if $n < r$) or $1, 2, \dots, r$ (if $n \geq r$). The probability of $p\{x, n\}$ of any value of $x \leq r$, for any value of n is given by*

$$p\{0, 0\} = p\{1, 1\} = 1$$

$$p\{0, 1\} = p\{1, 0\} = 0$$

$$p\{x, n\} = p\{(x-1)(n-1)\} \frac{r-x+1}{r} + p\{x, (n-1)\} \frac{x}{r}$$

*This simple recursive form is the only practical one; the general solution involves a complicated generating function which can only be evaluated by more arithmetic than is involved in use of the recursive expression.

while the probability $p_c\{x, n\}$ of any qualitatively distinct combination will be

$$p_c\{x, n\} = 1/\binom{r}{x} \cdot p\{x, n\}$$

An evaluation of the expression for $p\{x, n\}$, for $r = 5$ is given in table 1. While $p\{1, 1\}$ is unity and $p_c\{1, 1\}$ is $1/r$, for all higher values of n , $p\{1, n\}$ falls steadily. For values of x when $1 < x < r$, $p\{x, n\}$ first rises and then falls indefinitely; for $x = r$, $p\{n, x\}$ rises continuously, converging on unity as all the other probabilities fall.

TABLE 1
PROBABILITY TABLE, UNCERTAINTY AND NUMBER OF NICHES
FOR $r = 5$, $n = 1 - 11$

	$x = 1$ $\binom{r}{x} = 5$	2 10	3 10	4 5	5 1	$\Sigma I_{x,n}$	No. niches $p_1 = 0.001$
$n = 1$	1.000,00	1.61	5
2	0.200,00	0.800,00	2.66	15
3	0.040,00	0.480,00	0.480,00	3.10	25
4	0.008,00	0.224,00	0.576,00	0.192,00	...	3.13	30
5	0.001,60	0.096,00	0.480,00	0.384,00	0.038,40	3.08	28
6	0.000,32	0.036,68	0.345,60	0.499,20	0.115,20	2.84	26
7	0.000,06	0.016,13	0.231,17	0.537,60	0.215,04	2.57	26
8	0.000,01	0.006,50	0.148,38	0.522,55	0.322,56	2.22	26
9	0.000,00	0.002,60	0.092,93	0.477,39	0.427,08	1.94	21
10	0.000,00	0.001,04	0.057,32	0.419,08	0.522,56	1.68	17
11	0.000,00	0.000,42	0.035,02	0.358,19	0.606,38	1.45	16
Asymptotic to	0	0	0	0	1	0	1

We now interpret the size of the selection n , as a quantity dependent on the size of the organism inhabiting the environment. We also assume that each qualitatively different combination of elements corresponds to a different niche* and that each niche can be occupied by a single species, the specific properties of the niche being defined by the existence of interfaces between different kinds of mosaic elements. Thus if $r = 5$, then for $n = 1$, $x = 1$ there are five possible elementary niches (a, b, c, d, e) each having an equal probability of occurrence ($p_c = 0.2$). For $r = 5$, $n = 2$, there will be ten possible composite niches (ab, ac, ad, ae, bc, bd, be, cd, ce, and de); the probability of the selection comprising one of these arrangements is .800, the probability that it comprises any specified one is 0.080.

*We do not intend to offer this model as a complete theory of the niche but rather consider that each kind of mosaic element contributes various ranges to the values of the parameters of the niches defined in an intensive way, as for example, in Hutchinson (1958).

INFORMATION-THEORETIC INTERPRETATION

We may now compute the uncertainty $\Sigma I_{x,n}$ associated with any array of niches for a given value of n , where

$$I_{x,n} = -\left(\frac{r}{x}\right) p_c\{x, n\} \ln p_c\{x, n\}$$

or

$$\Sigma I_{x,n} = -\Sigma p\{x, n\} \cdot \ln \cdot p_c\{x, n\}$$

where summation is over the rows of the table. A plot of $\Sigma I_{x,n}$ against n gives a curve rising to a maximum at some value of n slightly less than r and then falling asymptotically to zero. This relationship is a formal quantitative expression of the fact that when $n = 1$ we know we have an equal chance of getting any one of the r kinds of elements and can get nothing more; when n is very large we are almost certain to get every kind of r elements in every selection, but for intermediate values of n , near $n = r$, we shall have great qualitative diversity. If we assume for the purpose of argument that the niches can be analyzed into mosaic elements, we are more likely to get a great diversity of niches and so of species, when we are dealing with organisms to which some intermediate size, measured as n , can be associated, than when the measure n is very small or very large.

EMPIRICAL INTERPRETATION

In order to put the theory in a form that can be compared with actual observations we have to consider three further specific points in interpretation. If we assume that potentially each niche available can support but a single species, and that n is some monotonic function of the size of the individuals of that species, the quantity n is still an unsatisfactory measure of the function. This is easily seen when we consider high values of n for which $p_c\{x, n\}$ approaches unity, implying that a single species can be present. It would be quite unrealistic to suppose that for each ascending value of n this single species is replaced by another. It is reasonable to adopt a geometric measure of the size function. This may be obtained by taking the modal size n_m and then regraduating in terms of $\phi^q n_m$, obtaining $\dots \phi^{-3} n_m, \phi^{-2} n_m, \phi^{-1} n_m, n_m, \phi n_m, \phi^2 n_m, \phi^3 n_m \dots$ as the intervals of the new measure, which is taken to be a measure of length.

The value of ϕ may be obtained by considering the phenomenon of *character displacement*. (Brown and Wilson, 1956). As is pointed out elsewhere by one of us (Hutchinson, *forthcoming*) for birds and mammals this phenomenon suggests that a value of $\phi = 1.3$ would ordinarily prevent complete competition between species.

Now considering some fairly large value of q , for which $p_c\{x, n\}$ is almost unity, we should intuitively expect but a single species almost certainly to be present, as is indicated by the information-theoretic approach. If we accept the assumption that but a single species is present, this in fact implies that there is a limiting probability p_1 such that when $p_c\{(r-1), n\} < p_1$, only the r^{th} column is of any significance. Intuitively it seems clear that the limiting probability must be smaller for a large fauna

than for a small fauna, but its value cannot be determined deductively. In any given case p_1 represents an empirical constant involved in fitting actual data to the theoretical model.

Another empirical constant is also needed, namely the value of r . Provided p_1 is sufficiently small (i.e. $p_1 \leq \sim 0.01$ for $r \geq 3$) the numbers of available niches will increase to a maximum at $n_m (\simeq r)$ and then after a shorter or longer plateau will decline irregularly to unity. The determination of r depends on the properties of the distribution up to the measure of modal size n_m . In table 2 the number of niches in the modal class (M), and the total number up to and including (A) or excluding (C) this class, is given for various values of r . We select from table 2 a value of r appropriate to

TABLE 2

r	$M = 2r - 1$	$A = (r + 2)2^{r-1} - r - 1$	$C = A - M$
1	1	1	0
2	3	5	2
3	7	16	9
4	15	43	28
5	31	106	75
6	63	249	186
7	127	566	339
8	255	1,271	1,016

the modal group and to the whole array of submodal groups. Since in dealing with part of a fauna, which will usually be necessary, there is always a possibility that niches can be apparently unfilled owing to competition of the smallest members of the part under consideration with the largest members of some other group (for example, small shrews and large carabid beetles), no great exactitude can be expected; all we can hope is to choose r in such a way to provide reasonably concordant values of M and B . Having obtained r , the appropriate probability table is constructed. Then by comparing the probabilities in the columns for $x < r$ with the observed distribution, an appropriate value of p_1 can be selected. Knowing p_1 we assume that all niches are filled if $p_1 < p_c\{x, n\}$, and that $\left(\frac{r}{x}\right) \frac{p_1}{p_c\{x, n\}}$ niches are filled if $p_1 > p_c\{x, n\}$. Fractional niches are rounded off to whole numbers or if $p_1 > 0.5 p_c\{x, n\}$, discarded.

EMPIRICAL SIZE DISTRIBUTION CURVES AND THE FITTING OF AN ACTUAL CASE

For several groups that have been tried (birds of Massachusetts, dragonflies of N.E. United States, terrestrial Heteroptera of Britain, Chaetognatha of the world ocean) the size distribution by species appears to be a roughly symmetrical logarithmic distribution curve without the kind of tail predicted by the theory. The case of the dragonflies is particularly instructive, because the separate distributions for the Zygoptera and Anisoptera are skewed in opposite directions, but when both groups are considered together a close approach to symmetry is obtained (figure 1). The two sub-

orders obviously compete in the region of the mode for the whole order. Only in the case of mammal faunas is there a distribution that is somewhat like that provided by the model. The ordinary symmetrical logarithmic curve we take to imply that a given type of organization implies a certain

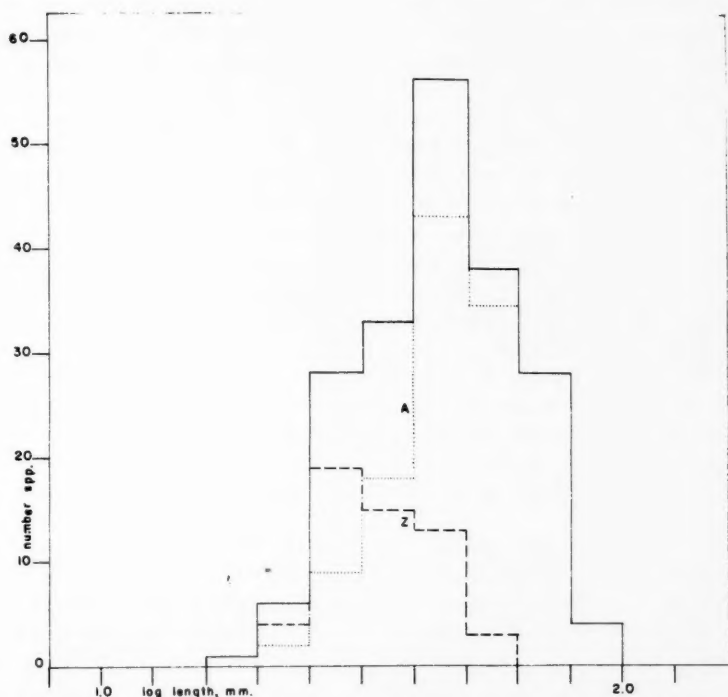


FIGURE 1. Size distribution of the species of Odonata of the northeastern United States (New England, New York, New Jersey, and Pennsylvania); A. Anisoptera separately Z. Zygoptera separately (data from Needham and Heywood (1929) for Zygoptera; Needham and Westfall (1955) for Anisoptera).

class of particularly appropriate niches and that as more extreme niches are occupied the amount of evolutionary displacement needed is about as easy to achieve, with a given organization, by a change in size of a given factor in either direction. In the case of the mammals the great diversity of structure appears to permit a far greater size range, even within the herbivorous level. We have proceeded with the analysis of two mammal faunas in the hopes that this class may provide a sort of model of the whole animal kingdom above a certain size. In selecting a fauna to analyze it is essential to choose a region small enough to exclude allopatric species, as these seem to be most developed in the families of small mammals. It

is also essential that the small species be well known, and that the total fauna be sufficiently large.

The first example analyzed is that of the western part of continental Europe, roughly Belgium and northwest France, corrected for species known to have been introduced since the Middle Ages, or exterminated within historic time* in either Britain or the adjacent continent (figure 2). The data on sizes (head and body length) were obtained from Miller (1912) and from Barrett-Hamilton and Hinton (1911-1921). The value of r was taken as 3, the modal interval $n_m - \phi n_m$ as 70-91 cms, with $\phi = 1.3$, while p_1 was taken as 0.005. In the second fauna (figure 3), namely that of the originally wooded part (excluding *Bison bison*) of Michigan (Burt, 1946) the same values for r and ϕ are used, but p_1 is evidently lower and was taken as 0.00001. It is realized that with the rather large number of constants involved, any sufficiently asymmetrical distribution would accord with the theory at least as well as the mammal fauna in question. The interest of the method is solely in showing how a mammal fauna of the observed kind *could* be built up with a very small amount of initial diversity if a sufficient size range is permissible.

Interpretation of ϕn_m and n . In the case of the mammals of Michigan for which the home ranges (R) are approximately known, it appears (figure 4) that omitting the very vagrant marten, the area of the home range (Burt, 1946) varies roughly as the square of the head and body lengths (B). This suggests that the values of the linear size categories are really measures of categories of \sqrt{R} .

The interpretation of n is more difficult. The Michigan data suggest that n_m , corresponding to $n = 3$, also corresponds to $R = 0.38$ acres or 1538 square meters. Though nothing has been postulated about the dimensions of the unit of n , it is evident that in this case one unit of n corresponds to a length of $\sqrt{1538/3}$ or 13 meters; each mosaic element may be thought of as having the area of a square of this side length. Superficially it is by no means obvious from what we know about mammalian ecology, how biotopes would be built up of mosaics of three different kinds of elements of this size. Since the theory does not require that the elements be simple, but merely different and repeated, this objection is not fundamental.

The interpretation of randomness. The most obvious criticism that can be made of the model is that the different kinds of mosaic elements are distributed at random according to the postulates on which the model is built. If we consider a case in which the kinds of elements are arranged in a highly superdispersed manner, the distribution will have no effect on the qualitative number of choices when n is small, but will greatly increase the probability of more or less uniform arrangements when n is large. The superdispersion in fact, to a first approximation, lowers the value of p_1 . It is perhaps reasonable to find that p_1 is evidently lower in Michigan, which

**Rattus norvegicus* excluded; *Castor fiber*, *Ursus arctos*, *Canis lupus*, *Lynx lynx*, *Martes foina*, *M. martes*, *Felis silvestris* and *Sus scrofa* included.

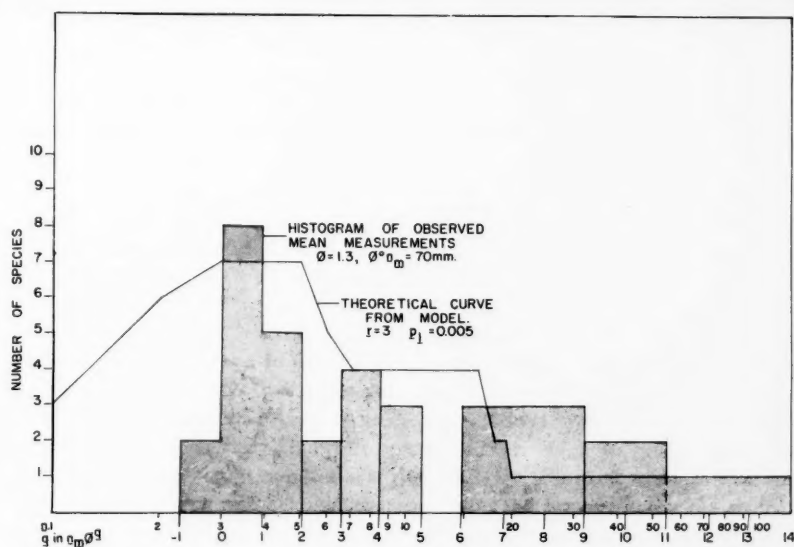


FIGURE 2. Mammals of western Continental Europe, with model curve for $r = 3$, $\phi = 1.3$ $p_1 = 0.005$.

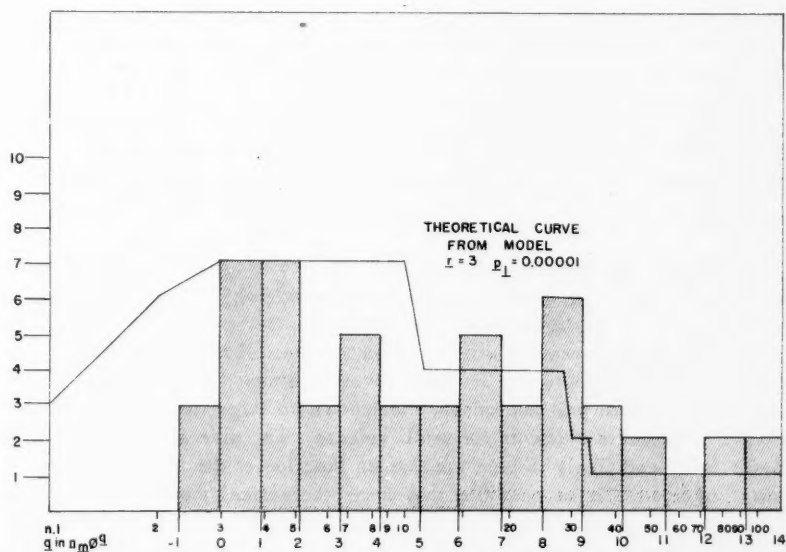


FIGURE 3. Mammals of Michigan, with model curve for $r = 3$, $\phi = 1.3$ $p_1 = 0.00001$.

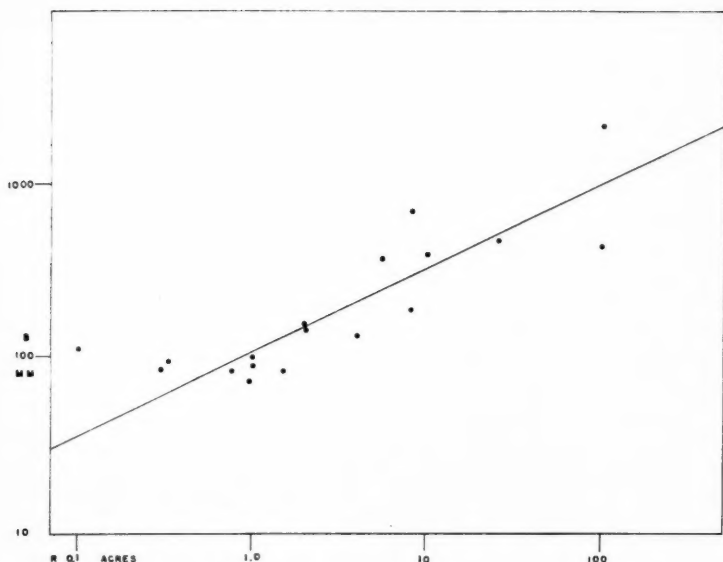


FIGURE 4. Relationship of logarithm of (B) mean head and body length (mm.) to logarithm of (R) home range (acres) for mammalian species in Michigan for which home-range is known; *Martes americana* (length 495 mm., range 6000-9000 acres) omitted. Data from Burt (1946). The straight line is fitted by eye with a slope of 1:2.

represented a much less disturbed habitat during the early 19th century than France and Belgium have probably provided at any time since the late Neolithic. It is quite likely that in reconstructing the natural western European fauna more large extinct species such as the aurochs, and possibly the tarpan, should have been added. Extinction of such large animals may in fact be attributed in a general way to a human randomization of the habitat.

GENERAL APPLICATION

In a certain sense the application of the theory to mammals tells us little that we did not know before, and is therefore trivial. The significance of the approach is in the fact that the mammalia, being a highly diversified group, may perhaps provide a model of the terrestrial fauna of a locality as a whole. Such an approach, however, involves a new difficulty. The postulated size of a mammalian mosaic element is so large that it must greatly exceed the mosaic elements for small insects. The size of the mosaic elements is indeed likely to be a continuous function of the size of the organisms involved. It is possible that some theoretical modification of the model involving the size measure might be developed, though at present we have not seen how to do this. In its present form the theory does at least suggest one possible if partial explanation of the way that sizes seem to be

distributed throughout whole faunas, and suggests the desirability of studying such distributions more intensively than in the past. It might be possible to gain further information by an intensive examination of the incidence of related sympatric species of similar size in various groups of large and small animals in different kinds of environment.

SUMMARY

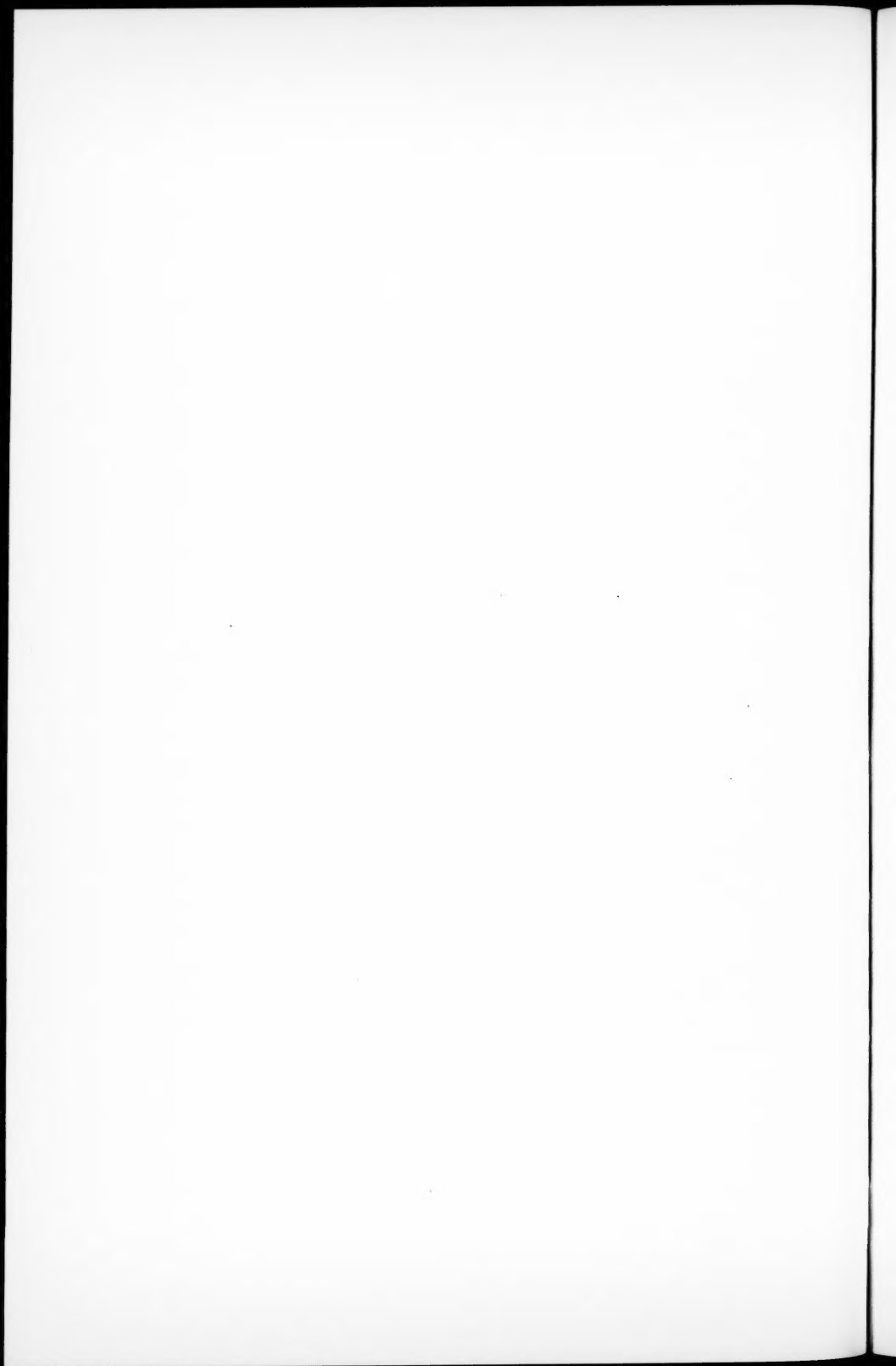
Even within a given level of the food web there appear to be fewer species of large than of small animals. A model can be constructed in which the properties of the niches of different species are defined by the numbers of kinds of interface between a limited number of sorts of randomly distributed environmental mosaic elements. This model implies few very small species, rapid increase in number of species up to a modal size and a slow decline in number, ideally asymptotic to unity, as the size increases. Structurally uniform groups of animals such as the Odonata do not show this distribution, but in mammal faunas it is approached. It is suggested that if a really complete faunistic list for a given biotope could be constructed the size distribution by species would approximate the form given by the model.

ACKNOWLEDGMENT

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COMPETITION BETWEEN SUNBIRD AND HONEYEATER
SPECIES IN THE MOLUCCAN ISLANDS

S. DILLON RIPLEY

Peabody Museum, Yale University, New Haven, Connecticut

During 1954, with the aid of grants from the Guggenheim Foundation and the National Science Foundation, I was able to spend several months on the northern Moluccan Island of Batjan, eastern Indonesia. This is one of a group of most interesting islands situated in an arc of active crustal movements, vulcanism, and general orogenic instability between the Sunda Island projections of the Asian Continent and the mass of the Sahul Shelf of Australia and New Guinea. The evidence from the distribution of the fauna points to these islands having been essentially an oceanic group. The land fauna is relatively depauperate, being composed of elements that have arrived adventitiously by what Simpson calls the "sweepstake" method from west or east.

More detailed comments on the islands await a general paper on the collection. Suffice it to say for now that Batjan Island, with an area of approximately 1255 square miles and a single mountain ridge reaching an altitude of 6000 feet above sea level, has a population of over one hundred resident bird species, the majority of which, or 67 per cent, show strong Australo-Papuan rather than Oriental affinities.

- SUNBIRD SPECIES

Two species of the Old World family of Nectariniidae, or Sunbirds, occur here. They are *Nectarinia jugularis* and *Nectarinia sericea*, and both range on into New Guinea and adjacent islands. These two species have spread into the Moluccas from the Philippines and Celebes (Sulawesi) *vide* Stresemann (1939-1940). The two species are virtually identical in size although markedly different in appearance. Their feeding habits appear to be identical, but it must be said that their ranges, although overlapping, are not identical. Where we observed the two on Batjan, *N. jugularis* was found in the coastal area from the edge of the sea to 350 feet altitude, while *sericea* was not observed below 350 feet above sea level, nor indeed much higher than 500-600 feet, where its favored biotope tended to disappear in the higher stands of tropical wet evergreen forest. Both species have a fairly long history in these archipelagos, having split into a number of recognizable subspecies, but both species are identified with man's occupation, being found almost entirely in gardens, coconut plantations, and scrub adjacent to human habitation.

TERRITORY

Both species of sunbirds have territories. I was able to observe two pairs of *N. sericea* on two territories. These birds occupied adjacent areas of

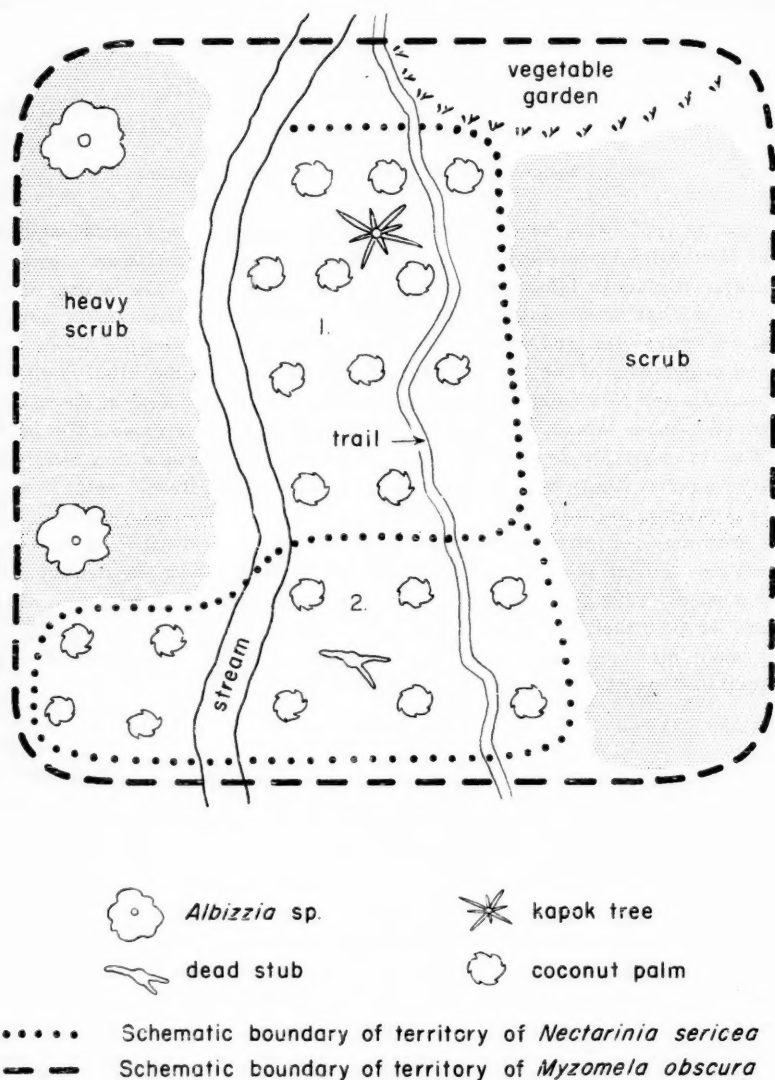


FIGURE 1. Approximate territories (1, 2) of two pairs of Purple Sunbirds on Batjan Island.

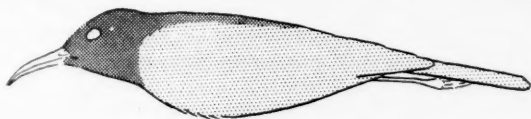
coconut plantation bordered by heavy scrub as shown in text figure 1. Here may be seen an approximate area three quarters of an acre to two acres for each pair. The two male Black Sunbirds were observed chasing rivals out of their territory. After each foray, which consisted of threat and loud singing, the bird would return to its singing post. In *sericea*, the male displays to the female by singing a variety of small tinkling runs, far less true musi-

cally, and less canary-like than those of *jugularis*. This display is accompanied by wing flapping. A male in territory number one displayed several times to a female who also sat in the display tree. The female flew away after he had moved several times to higher perches above her. This display was carried on at the feeding sites, the coconut palms in the territory. These two species feed on the flowers of the coconut palm, taking nectar and small insects attracted to the flowers, as well as on flowering shrubs in the cultivated or semi-wild gardens.

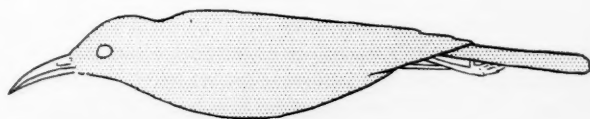
HONEYEATER SPECIES

Two species of Honeyeater occur on Batjan, belonging to the family Meliphagidae of Papuan-Australian origin. Both have reached the Moluccas from New Guinea and its adjacent western islands, this area marking the farthest western spread of these species. Both species are differentiated

Myzomela
sanguinolenta



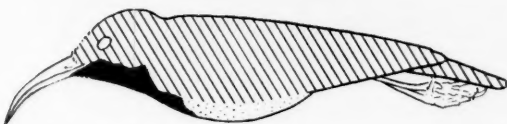
Myzomela
obscura



Nectarinia
sericea



Nectarinia
jugularis



■ red ■ brown ■ black ■ olive ■ yellow

FIGURE 2. Outline sketch of two species of honeyeaters and two species of sunbirds to show comparative size.

into several subspecies indicating long residence in this area. *Myzomela obscura* is the lowland species, found from sea level to approximately 350 feet. It is replaced in the mountains, normally above 2500 feet, by *Myzomela sanguinolenta* which is similar in size, but brightly colored; text figure 2.

Except at the feeding trees, honeyeaters were always seen individually as solitary birds. It would appear from our observations at least that the population of *M. obscura* is relatively small and is spread out widely and thinly over the lowlands of Batjan. Only at the large, umbrella-like flowering trees of *Albizzia molucca* was it ever possible to see more than two individuals of this species together. On these occasions, the air was full of sharp "chit" or "tsit" noises, and very active chasing was seen. The impression we received was that the honeyeater is a relatively unsocial species, whose range is not easily compressible, and thus a small population appears to be spread over a wide area. The honeyeater feeds on the flowers of forest trees as well as the coconut palms and garden shrubs, taking nectar and small insects attracted to the flowers.

COMPARISON OF THE SPECIES

The above brief description indicates that here on an island such as Batjan, occupying an interstitial position between two faunal regions, it is possible to observe the contrast in behavior and habits of species of differing phylogenetic origin but of similar requirements. The two species of sunbird and one honeyeater are of similar size and have closely similar food requirements. The sunbirds appear to occupy virtually identical niches with slight altitudinal separation, thus providing a buffer between them to counteract the zone of overlap. Although their ranges coincide, they are not totally sympatric and thus are not in complete competition in the sense of Lack (1944). These species seem numerically very common.

Habits and food requirements indicate that the honeyeaters have evolved to exploit a niche equivalent to that of the sunbirds. Comparison of the species on Batjan shows the size of these birds to be similar. Sunbirds derive their nectar supply by a probing tubular tongue, while honeyeaters secure their nectar by a brush-tipped tongue. Otherwise, there is no basic morphological difference between them.

COMPETITION

Birch (1957) defines competition as occurring "when a number of animals of the same or of different species utilize common resources the supply of which is short or if not in short supply, competition occurs when the animals seeking that resource nevertheless harm one or other in the process." Competition in a certain sense occurs between the honeyeater and the two species of sunbirds under Birch's Category V, "the number of other organisms of different species, non-predators which utilize the same resources." The following observations indicate to me that competition in some form is occurring here. Salomonsen (personal communication) substantiates this by

pointing out that on very small islands where the total available biotope is too limited or compressed only the honeyeater or the sunbird but not both occur although within the range of both species. Thus, on Ninigo Island to the east, only the black honeyeater, *Myzomela nigrita*, occurs, although *N. sericea* and *jugularis* occur on large nearby islands.

It may be worthwhile here to describe the contacts between *Myzomela obscura* and *Nectarinia sericea* in a territory, (number one, see figure 1), with a male *N. sericea*. During the period September 25–October 2, our camp was pitched in territory number one. The male sunbird, *sericea*, had his display post in a kapok tree in the center of this territory. On four different days during this period, although the male *sericea* was in full possession of the territory, actively chasing the male of territory number two, I saw this pair of sunbirds, male and female, chased away from their own feeding trees, coconut palms within the territory, by a male honeyeater. During the time that the honeyeater, *M. obscura*, was in territory number one, the rightful owner, the sunbird, allowed himself to be chased, perching quietly in a hunched position, completely subservient to the honeyeater which fed casually throughout the territory.

As soon as the honeyeater had departed, the male *sericea* flew to his display tree, and after busy, well-nigh excessive preening, perhaps a displacement activity, would sing and display.

From these observations, it would appear that when males of the honeyeater and the sunbirds occur together during the breeding season, the honeyeater appears to be dominant even though within the territory of the sunbird. But it also appears that the honeyeater population is low, their territories presumably large, and individuals wide-ranging within their home range. What factors can be occurring here to create a balance between the population of the honeyeater and the very common, though localized, sunbird?

Pitelka (1951) has discussed competition between species of hummingbirds in California. Two species, *anna* and *sasin*, occur together. Where their territories overlap, in areas of willows preferred by *sasin*, an attempt at a census of the populations shows that a mutual but unbalanced depression of population levels of at least males occurred. In this interaction, the larger, more aggressive species, *anna*, was favored. But in spite of this success and the prevalence of *anna* males, a five-year census of a particular canyon near Berkeley failed to reveal any nests or fledglings of this locally dominant species.

On the other hand, *sasin* males were less dominant and occupied a smaller numerical ratio in the proportion of two to nine, or 48 per cent of occupation of available territorial nesting sites, compared to 80 per cent occupation for the males of *anna*. Pitelka assumes this to be a significant difference. At the same time that no nests of dominant *anna* were discovered, five nests of less dominant *sasin* were observed. The relative ease of observation of *anna* can only favor the validity of this observation. Although *anna* males were more aggressive and more successful, actual nestings were infrequent.

Udvardy (1951) does not feel that intolerance between the individuals of different species results in replacing one of two species by the other. He

does not feel that this is true competition. Yet, he points out, "such struggles take time and if they recur frequently during the period of reproduction, breeding, feeding of the young, etc. will be neglected and this might locally lead to reduced capacity of reproduction of the species concerned."

An interesting example of this is that of Hagen (1947) who, studying a pair of small falcons (merlins) on the nest, found that the incessant aggressiveness of a fieldfare nearby resulted in unsatisfactory hatching of the fieldfare brood. Thus, the more aggressive species can suffer by its behavior. It may well be, as suggested by MacArthur (1957), that interspecific relations of this sort may serve as a type of density-dependent phenomenon, effective in regulating the abundance of the species. Thus competition can be reduced. In the absence of predators or other density-independent events, a greater absolute survival value may be derived from a limited reproductive success as shown by Lack (1954). Aggressiveness may thus be an important factor, not only in spacing out territory in an intraspecific sense as noted by Tinbergen (1952), but it may also have a density-dependent effect in interspecific competition.

SUMMARY

Observations of unrelated but ecologically comparable species of sunbirds, Nectariniidae, derived from Malaysia, and honeyeaters, Meliphagidae, derived from Australia in the interstitial region of the eastern Indonesian islands, indicate that these birds of identical size and similar food habits, are at least in partial competition.

A study of the behavior of these birds in the territory of one of the species indicates an unequal numerical ratio between the species and dominant, aggressive behavior by the scarcer species (honeyeater). It is suggested that the behavioral activity of aggressiveness may in itself serve to limit successful reproduction in addition to other phenomena such as clutch size or nesting success of which so far nothing is known. Any activities of a social or behavioral nature which may serve to limit the reproductive rate of the species may, therefore, have a considerable absolute survival value.

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APPENDIX

ON THE THEORETICAL SIGNIFICANCE OF AGGRESSIVE NEGLECT IN INTERSPECIFIC COMPETITION

G. E. HUTCHINSON AND ROBERT H. MacARTHUR

Osborn Zoological Laboratory, Yale University, and Division of
Biology, University of Pennsylvania

In the preceding paper Dr. Ripley's fascinating observations raise the question as to the general significance of what may be called *aggressive neglect*, or the tendency of one species to neglect its brood, owing to the release of excessive aggressive behavior due to the presence of a second species.

We assume that when the population (N_2) of the second species is zero, no aggressive neglect will take place, and that when N_2 becomes very large the phenomenon will practically prevent reproduction by the first species. The natural form to express this relationship is obviously an exponential one. We suppose therefore that the birth rate in the population at any time is given by $b_1 e^{-pN_2}$, where p expresses the intensity of aggressive neglect. The birth rate will thus be b_1 when N_2 is zero and will approach zero as N_2 becomes very large, thus satisfying the biological requirements. So long as the function N_2 varies monotonically between 0 and 1, some departure from the exponential form will have no effect on the qualitative conclusions to be drawn. We assume the death rate is entirely density-dependent, of the form $d_1(qN_1 + rN_2)$. We write for the first species

$$\frac{dN_1}{dt} = N_1 b_1 e^{-pN_2} - N_1 d_1 (qN_1 + rN_2)$$

Now approximating e^{-pN_2} by $(1 - pN_2)$ we obtain

$$\frac{dN_1}{dt} = N_1 b_1 (1 - pN_2) - d_1 q N_1 - \frac{d_1 r}{b_1} N_2$$

Since when $N_1 \neq 0$, $b_1 \neq 0$, $N_2 = 0$ and $\frac{dN_1}{dt} = 0$

$N_1 = K_1$, the saturation population of the first species,

$$K_1 = \frac{b_1}{d_1 q}$$

writing $\alpha = \frac{r}{q}$ and $\gamma = \frac{b_1 p}{d_1 q}$

$$\frac{dN_1}{dt} = \frac{N_1 b_1}{K_1} \{K_1 - N_1 - (\alpha + \gamma)N_2\}$$

Similarly for the second species $\frac{dN_2}{dr} = \frac{N_2 b_2}{K_2} \{K_2 - N_2 - (\beta + \delta)N_1\}$

In these equations α and β are ordinary competition coefficients, while γ and δ may be termed *coefficients of aggressive neglect*.

If we assume that both species inhabit the same niche and that the coefficients of aggressive neglect are negligible, one species will displace the other according to the Volterra-Gause principle. Suppose that the first species is always displaced by the second. We then know that $\alpha > \frac{K_1}{K_2}$, $\beta < \frac{K_2}{K_1}$.

Suppose now that δ , rather than being negligible, has a positive value such that $\alpha > \frac{K_1}{K_2}$, $(\beta + \delta) > \frac{K_2}{K_1}$; this corresponds to the case in which each species has a greater adverse influence on individuals of the other than on those of its own species. In such cases, which seem to be rare save among antibiotic-producing lower organisms, the final outcome of competition depends either on the initial conditions or on the random occurrence of differential death which is not density-dependent. A certain indeterminacy will be apparent in field observations, even at equilibrium, if the complete histories of the populations are not known.

Dr. Ripley's admirable field data appear to suggest an explanation of his observed cooccurrences which is very illuminating with regard to ecological theory. Dr. Ripley has observed that *Myzomela obscura*, though it has large territories and a sparse population, is unevenly distributed in the lowland biotope of Batjan since some concentration of the birds appears on Albizzia trees. If we consider the aggressive behavior of the birds in the light of the above theory, we may conclude that there will always be areas where competition can go in favor of *M. obscura* and other areas where the process is in favor of *Nectarinia sericea*, simply owing to the variations in density of the two species in a context where such variations in density may determine the direction of competition. But since the variation in density is determined in Batjan to some extent by the habitat preferences of the birds, the two species do not, in the most vigorous abstract sense, occupy identical niches, and so their occurrence together raises no fundamental objection to the Volterra-Gause principle. This analysis of a very curious and illuminating case is offered primarily in the hope that it will stimulate more accurate thinking on such problems. We are greatly indebted to Dr. Ripley for the opportunity to consider the matter and to Dr. Jack Cunningham for discussion of some of the mathematical aspects of this type of case.

LETTERS TO THE EDITORS

Correspondents alone are responsible for statements and opinions expressed. Letters are dated when received in the editorial office.

THE MUTAGENIC ACTIVITY OF CAFFEIN IN DROSOPHILA

Extensive work has been carried out on the ability of various chemicals to induce mutations and in some cases these chemicals are also known to be carcinogens. The exact nature of the relationship between mutagenic and carcinogenic ability is not clear, but such a relationship is undoubtedly of great importance for an understanding of both phenomena.

The object of this communication is to draw attention to caffein, as a mutagen and a possible carcinogen. Previous work on the genetic effects of caffein has been of two kinds.

1. Kihlman and Levan (1949) have used caffein in the *Allium* test, and have demonstrated its ability, in subtoxic concentrations, to cause chromosome breakage in mitotic cells of the root tip. They also observed types of tumor induction following caffein treatment. Kihlman (1952) attempted to determine more specifically the seat of this radiomimetic ability, and found that it appeared to be dependent on the molecule as a whole.

2. Genetic effects of caffein have also been demonstrated in microorganisms: Witkin (in Demerec, Wallace and Witkin, 1948) and Gezelius and Fries (1952) have shown that it is able to induce mutations to phage resistance in *E. coli*, and back mutations to streptomycin non-dependence have also been induced in that organism (Demerec, Bertani and Flint, 1951). Physiological alterations in *Ophiostoma* due to caffein treatment have been shown to be of the nature of gene mutations (Fries, 1950).

In view of the apparent lack of information on the biological activity of this drug in *Drosophila melanogaster*, some experiments have been carried out to determine whether it is mutagenic in this organism. The incidence of sex-linked recessive lethals, as exhibited by the Muller 5 technique, was used as an index of mutagenicity. Males to be tested were from a Canton S stock. Each was mated daily with Muller 5 virgins, three to seven days old; five virgins were supplied each day for the first three matings, and three virgins for each of the following eight days, after which the males were discarded. Thus the sperm produced were separated into 24-hour broods, so that any differential response during spermatogenesis might be detected. In series I the test males had been reared on treacle-semolina-agar culture containing 0.25 per cent caffein. The medium was not seeded with yeast, thus ensuring that the larvae fed on the medium itself. This practice prolonged the developmental period by three to four days. However, work by

Olenov (1941) indicates that this delay in development is not likely to increase the spontaneous mutation rate. The first mating was made with males which were from zero to one day old. In series II, males less than 24 hours old were injected with a 0.5 per cent solution of caffeine in saline, and were mated approximately 18 hours later for the first brood. The P and F₁ generations were raised at 25°C., while the F₂ generation was raised at 20°C.—the difference being solely in order to make the best use of available space in constant temperature rooms. Any suspected lethals found in the F₂ were tested through another generation, at least 50 offspring of the F₃ being scored. In an F₃ sample of this size the absence of wild-type males is then highly significant, $p = 0.001$.

TABLE 1
SEX-LINKED RECESSIVE LETHALS INDUCED BY 0.25 PER CENT
CAFFEIN FOOD. FORTY-ONE MALES TESTED

Broods	1	2	3	4	5	6	7	8	9	10	11	Total
Number of X chromosomes tested	125	517	587	590	587	638	601	600	554	559	572	5830
Number of sex-linked lethals	1	6	5	5	3	0	3	5	2	9	0	39
Percentage of sex-linked lethals	0.8	1.2	0.9	0.5	0.5	0	0.5	0.8	0.4	1.6	0	0.7

TABLE 2
SEX-LINKED RECESSIVE LETHALS INDUCED BY INJECTION OF
0.5 PER CENT CAFFEIN SOLUTION INTO FORTY-TWO MALES

Broods	1	2	3	4	5	6	7	8	9	10	11	Total
Number of X chromosomes tested	412	366	597	566	536	552	577	557	552	467	513	5695
Number of sex-linked lethals	4	0	5	7	0	9	7	1	0	0	0	33
Percentage of sex-linked lethals	1.0	0	0.8	1.2	0	1.6	1.2	0.2	0	0	0	0.6

Tables 1 and 2 show the numbers of chromosomes tested and the lethal mutation rate for each brood for series I and II respectively. In the case of series II, there was marked heterogeneity of response between the injected males.

The spontaneous mutation rate for sex-linked recessive lethals was determined for the stock used; from sperm produced during the first nine days

of adult life, 4411 X-chromosomes were tested and six lethals found, giving a mutation rate of 0.14 per cent. It may therefore be concluded that caffeine is weakly mutagenic in *Drosophila*. There appears to be no marked fluctuation in sensitivity correlated with stage of development of the organism (this would be shown up in differences between broods in series I); however, series II indicates that later stages in spermiogenesis may be more susceptible than pre-meiotic stages. Caffeine is apparently not altered by processes of digestion and absorption in higher organisms, and this may be assumed for *Drosophila*. It is probable that, when ingested with the food, it reaches the testis unchanged. The induced mutation rates are not very high, but for comparative purposes it is useful to remember that a sex-linked lethal mutation rate of 1 per cent in mature spermatozoa is induced by 250 roentgen of X-radiation (Edington, 1956).

In considering the cytochemical implications of caffeine mutagenesis, recent investigations on *E. coli* by Novick (1956) are of interest; he found that relatively low concentrations of some purine nucleosides (adenosine in particular) were able to suppress completely the activity of caffeine and many other purines. These purine nucleosides could also suppress two-thirds of the spontaneous mutation rate, but had no effect on the mutagenic action of ultraviolet or gamma-radiations. Thus it seems likely that at least part of the spontaneous mutation rate may be due to a process similar to the introduction of certain purines—Novick has tentatively postulated a "spontaneous purine" as a metabolic product. This work has also shown that caffeine does not simply increase (e.g. by metabolic stimulation) the incidence of mutation of the "spontaneous" type, as adenosine renders caffeine completely ineffective, but only partially reduces the spontaneous mutation rate.

Since caffeine has now been shown to be mutagenic in bacteria, fungi and *Drosophila*, it may well prove to be mutagenic, and perhaps carcinogenic, in man. Repeated small doses of this drug may, in the long term, compensate for its intrinsically weak mutagenic activity. However, further work is required before we can view this new genetic hazard in its proper perspective.

ACKNOWLEDGMENTS

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LESLEY E. ANDREW

DEPARTMENT OF ZOOLOGY
UNIVERSITY OF MELBOURNE
AUSTRALIA
October 20, 1958

AN EARLY DEFENSE OF DARWINISM

In this, the centenary year of Charles Darwin's *Origin of Species*, it is interesting to look back upon the reception of his work by the scientific men of the time and of subsequent years. Much has been written and said pro and con concerning Darwinism in the past century. The writer recently encountered a letter¹ which illustrates the struggle early pro-Darwinists had to advance their views.

This letter was written by William T. Sedgwick who at the time was a professor of biology at the Massachusetts Institute of Technology and biologist to the Massachusetts State Board of Health. He was primarily a bacteriologist, but was well known as co-author of the General Biology text written with E. B. Wilson. Some years after the letter was written, Sedgwick became president of the American Society of Naturalists (1901).

The recipient of the letter, Edward S. Morse, was at the time director of the Peabody Academy of Science, later known as the Peabody Museum of Salem. He had, on many occasions, written and lectured in defense of evolution. At the Buffalo meeting of the American Association for the Advancement of Science in 1886 he gave his presidential address on the subject of Darwinism. The following year at New York City he delivered as his retiring presidential address a review entitled, "A Decade of Evolution."

Mentioned in the letter is Alpheus Hyatt, a fellow student of Morse under Agassiz and a former colleague at the Peabody Academy of Science where the two with other co-workers had founded the American Society of Naturalists and the *American Naturalist* (*Amer. Nat.* 68: 385-401, 1934; 78: 29-42, 1944; 90: 209-225, 1956). Both Morse and Hyatt avidly followed the teach-

¹Acknowledgment is expressed to Mrs. Catharine Robb Whyte, granddaughter of E. S. Morse, and to Ernest S. Dodge, director of the Peabody Museum of Salem, Massachusetts, for permission to study the Morse Correspondence and to quote the letter used in this note.

ings of Darwin rather than the anti-Darwin views of Agassiz. Hyatt also published many evolutionary studies, and these became the central theme of his life's researches. It is surprising that he took the stand attributed to him in the letter. It is possible that he might have been misunderstood, or that he was arguing a detailed point rather than making a general statement as claimed.

The other person mentioned in the letter was John W. Powell, director of the U. S. Geological Survey at the time. He had become famous for being the first to explore the Grand Canyon by boating down the Colorado River. He had written a volume on *Human Evolution* and another on *Three Methods of Evolution* (1883). He followed Morse two years later as president of the American Association for the Advancement of Science (1888). The complete letter, which indicates the problem pro-Darwinists have long faced, is reproduced below.²

RALPH W. DEXTER

DEPARTMENT OF BIOLOGY
KENT STATE UNIVERSITY
KENT, OHIO
December 3, 1958

²Massachusetts Institute of Technology

Boston, March 5, 1888

Dear Prof. Morse,

I hope that if you can make it handy to do so you will tell the audience Wednesday evening a word or two in favor of Darwin and Darwinism. Powell pitched right and left into Spencer and scouted the idea that the environment has had any great effect upon man's development from savagery, while Hyatt assailed the notion that a struggle for existence is a universal fact. (I suppose he meant to say Natural Selection, but he actually did say struggle for existence).

I find in short that with these vigorous attacks upon Darwinism and no defenders, our cause bids fair to muddle, as it has already mystified a lot of the "laity". For Heaven's sake then do give them a little sound evolutionary doctrine and don't fail to say, "As is agreed by all but a very few" F. S. K. Let us not have Darwinism trodden on without at least an answer.

Truly yours,

W^m. T. Sedgwick

A GENETIC COMPONENT OF VARIABILITY IN ERYTHROCYTE
SEDIMENTATION RATE*

In reviewing the laboratory reports obtained as a part of medical examinations given to adult twins and their available single-born siblings by Osborne and De George, a remarkable agreement in the erythrocyte sedimentation rates (ESR) between the two members of monozygotic twin pairs was noted. This observation suggested the possible interest of an analysis of the ESR in this adult twin population which had been evaluated as to health status.

Blood specimens had been obtained from both members of every twin pair simultaneously, and their ESR determinations performed by the same technician, employing the Westergren method. Neither the relative health status of the subjects, nor the twins' zygosity was known at the time these determinations were performed.

On the basis of medical examinations, all subjects utilized in this analysis were judged to be in essentially good health. The range of the ESR values used in the present analysis were: from 1-10 mm/hr. for males, and from 1-20 mm/hr. for females. Sibling pairs have been obtained by pairing two single-born sibs, or by randomly pairing one member of a twin pair with a single-born sibling; only like-sex pairs have been used. ESR determinations have been analyzed for: 30 pairs of male twins, (21 monozygotic and nine dizygotic pairs), and six male sibling pairs; 49 pairs of female twins, (27 monozygotic and 22 dizygotic pairs), and 12 female sibling pairs. For the diagnosis of zygosity, extensive serological and morphological characters were used; the method will be described elsewhere by Osborne and De George. The statistical analysis of the data is based upon a mean intrapair variance ($1/2n\sum x^2$), where n is equal to the number of pairs, and x is the difference between the two members of a pair in mm/hr. Variance ratios are calculated and the F Distribution used to obtain the probability levels of these ratios.

In both male and female monozygotic twins small mean intrapair variances are found (table 1). In females the difference between the mean monozygotic and dizygotic variances is highly significant ($P < 0.001$). In males this comparison fails to provide a statistically significant F ratio, though the mean dizygotic intrapair variance is twice as great as that found for monozygotic male pairs. The possibility of a chance occurrence of too small a male dizygotic variance with these small numbers is indicated by the much larger male sib variance. If the male dizygotic variance and the male sib variance are combined for comparison to the monozygotic twin variance, an F ratio of 3.91, ($P < 0.005$), is obtained.

*This study was supported by the Commonwealth Fund of New York and was carried out within the facilities of the Columbia-Presbyterian Medical Center.

The greater variability of females relative to males for the erythrocyte sedimentation rate is a well-known phenomenon (Wintrobe, 1956). In view of this, the extremely small female monozygotic mean intrapair variance is of particular interest. Agreement between the two members of monozygotic twins was commonly found throughout the range of determinations. For example, in one monozygotic pair both members had an ESR of 3 mm/hr. and in another pair 16 mm/hr. in contrast to the dizygotic twins in which the ESR of one member was 17 and that of the co-twin was 4 mm/hr. In another dizygotic pair the rates were 19 and 7 mm/hr. The present data indicate that

TABLE 1
INTRAPAIR DIFFERENCES IN ESR

		n	Variance	F	P
♀	MZ	27	1.889	9.15	<.001
	DZ	20	17.275	1.05	>.25
	Sib	12	18.083		
♂	MZ	21	1.024	2.01	<.10
	DZ	9	2.056	3.36	.05
	Sib	6	6.917		

MZ = monozygotic twin pairs.

DZ = dizygotic twin pairs, (like sex).

Sib = sibling pairs, (like sex).

variability in the erythrocyte sedimentation rate of adults in essentially good health is genetic. Although a twin method does not provide information regarding the genetic mechanism which may be involved, there is an implication that the manner of inheritance is relatively simple and strongly sex-influenced. If the genetic component of variability in sedimentation rate is as strong as is suggested by this twin data, it may in part account for the variations observed in the ESR within a given pathological state. Consequently, further investigation of possible individual genetic differences for normal sedimentation rates may greatly increase the diagnostic value of the ESR.

By the use of a twin analysis it has been possible to demonstrate that in adults in essentially good health the erythrocyte sedimentation rate has a measurable component of genetic variability. While the nature of this genetic action cannot be determined by a twin analysis, the indication for further genetic study is clearly suggested.

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RICHARD H. OSBORNE
FRANCES V. DE GEORGE

INSTITUTE FOR THE STUDY OF
HUMAN VARIATION
COLUMBIA UNIVERSITY
NEW YORK
November 26, 1958

Present address: Sloan-Kettering Institute, 410 East 68th Street, New York 21, New York.

SELECTION FOR INCREASED RECOMBINATION IN
Drosophila melanogaster—A CORRECTION

A letter by Parsons (1958) to this journal described the effect on crossing over of using only recombinants between two closely linked loci as parents for several generations in *Drosophila melanogaster*. He observed a significant increase in the recombination fraction between the two loci after nine generations of selective mating of this kind and concluded that "these results confirm those of Pritchard and Calef."

This conclusion is based on a misunderstanding of our experiments with *Aspergillus nidulans*. In a sample of products of meiosis we considered only those which were recombinants for a very short interval. Among these, the recombination fraction in adjacent intervals was found to be very much greater, by a factor of over 100 in some cases, than in the sample as a whole. In order to obtain a sufficient number of recombinants to make an adequate comparison, it was necessary to make use of a technique which would automatically screen out ("select") recombinants from the sample irrespective of their frequency. For this purpose we used nutritional markers and plated on media which would permit the growth only of recombinants.

Parsons's data are of interest in that they show that the frequency of recombination in a given interval can be changed by selective breeding over a number of generations. What our experiments show, on the other hand, is that recombination events are not distributed at random over the genome but tend to occur in clusters. These clusters, or correlated recombination events, are restricted to minute segments of the genome and we were able to detect them only by making use of automatic screening techniques. The two types of experiment are quite unrelated and cannot be compared.

The misunderstanding has arisen through Calef's description of his results, which is in places ambiguous in that it can be taken to imply a causal

relationship between the selection of recombinants and the increases in recombination fractions observed. The nature of his experiments is made quite clear in the text, however. Each experiment was confined to a single sample of products of meiosis. There could therefore have been no causal relationship of the type assumed by Parsons, and no selection, in the sense of using a selected fraction of the progeny of one generation as parents of the next. In my paper the word selection was not used in the text.

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R. H. PRITCHARD

DEPARTMENT OF GENETICS
THE UNIVERSITY
GLASGOW, SCOTLAND
January 10, 1959